VOL THREE / ISSUE TWO

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ORIGIN, EVOLUTION, EXTINCTION

THE EPIC STORY OF LIFE ON EARTH

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LIFE ON EARTH: ORIGINS, EVOLUTION, EXTINCTION

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Aixsponza

Life story

HOW did life begin? This is one of the eternal questions. All cultures have a creation story, but modern science has the best one of all – a near-complete account of how our planet went from a barren lump of rock to one covered in a rich diversity of plants, animals and microbes.

For almost a billion years after it formed, Earth was a lifeless place with hellish conditions. But around 3.8 billion years ago, after the surface had cooled and oceans formed, something amazing happened. Out of Earth's primordial chemicals arose an entity capable of replicating itself. Life was born. The rest, as they say, is prehistory.

The forces of evolution worked on this simple life form and its descendants to create all manner of useful adaptations including a system to capture energy from the sun (photosynthesis), biological computers (brains) and even a biological wheel.

We will probably never know exactly how this first life arose or what it was like, but there are many other mysteries we can hope to solve. This issue of *New Scientist: The Collection* tackles these questions. It tells the epic story of the only living planet we know of in the universe, from life's origins to the watershed moments in its history.

Chapter 1 is about the dawn of life. Charles Darwin imagined that life arose in "some warm little pond", but there are many other possible cradles of life. Where and when did it happen? What ingredients were needed, and was the event inevitable?

Chapter 2 explores the key steps in the early development of life. For the first 1.5 million years of its existence, life consisted of simple microbes, but then things got more interesting. Cells developed internal "organs" and multicellular life eventually followed. What drove this process? What were the first complex creatures on Earth, and what drove the successive explosions of evolutionary creativity?

Chapter 3 takes a tour of the most fascinating fossils ever discovered, including feathered dinosaurs and myriad other long-dead creatures. What can we learn about the behaviour of animals from their fossilised remains, and where can we find "missing links" that tells us about key transitions such as how birds took flight?

In Chapter 4 we take a look at Gaia theory, tackling the controversial question of whether our planet acts like a giant organism, capable of regulating its own environment.

Chapter 5 is all about the unifying theory of life. Although the beautiful and simple idea of evolution by natural selection was first put forward in 1858, many myths and misconceptions about it still persist. We tackle them head on.

Where there's life, there's death. This is the appropriate subject of our final chapter: extinction. The fossil record reveals that most species that existed have gone. Why? What were the biggest mass extinctions? And what would our planet look like if all life suddenly died?

Prepare to go on a journey of a lifetime.

Alison George, Editor

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Extinction

Red alert for the Sumatran tiger. Fauna & Flora International seeks action from New

PHOTO: EUAN BOWEN-JONES/FFI

This Critically Endangered tiger has been pushed to the edge of extinction. You can help save it by donating right now to Fauna & Flora International. Visit www.FFIsumatrantiger.org or cut the coupon below.

One of the Sumatran tiger's final strongholds is under threat from a massive onslaught from poachers. Without action now, this extremely rare big cat faces imminent extinction. Latest figures confirm there are only 350 Sumatran tigers left. We must act now to save them.

- **£83,131 is needed to help us fund more rangers and step up action against the poachers in Kerinci Seblat National Park.**
- **This is one of the final strongholds of the incredibly rare Sumatran tiger, a place where the battle to save the Sumatran tiger will be won or lost.**
- **FFI's work here could be all that stands between the Sumatran tiger and extinction.**
- **The £83,131 needed to fund this urgent work must be raised immediately.**

A 600% increase in snares laid since 2011 has put FFI's anti poaching team on red alert. Habitat loss has already pushed the Sumatran tiger to the brink of extinction but to make matters worse, poachers have stepped up their efforts to snare these magnificent cats.

Fauna & Flora International (FFI) has put out an urgent call to the global community to save the last Sumatran tigers currently existing in the wild – and specifically to employ more rangers. There are now only around 350 Sumatran tigers left.

FFI is urgently seeking funds to step up their crucial conservation programme in Kerinci Seblat National Park, Sumatra, Indonesia. In order to safeguard the future existence of these magnificent creatures, it is imperative that more rangers are employed.

PHOTO: GILL SHAW

"If you value the natural world – if you think it should be protected for it's own sake as well as humanity's – then please support Fauna & Flora International."

Sir David Attenborough, OM FRS Fauna & Flora International vice-president

The fact is that, right now, the Sumatran tiger faces a number of very serious threats, which are putting their very survival in jeopardy. And, sadly, they are all man-made.

Poaching is a constant danger for the elusive Sumatran tiger – and now poachers have stepped up their efforts. Hunters make good money from the tiger's beautiful skin, which remains in great demand as a status symbol across Indonesia and beyond. Also, its bones are illegally exported to use as ingredients in traditional Asian medicines.

What is really worrying now is that poachers have increased the number of tiger snares laid by 600% since 2011 and the number of snares found have been at record levels.

This is against a backdrop of a very serious loss of habitat. In the last 10 to 15 years, natural forest cover in Sumatra has been slashed by almost a staggering 40%. And recently, great swathes of forest have been consumed by fire, destroying more of the forest habitat..

It is clear why these majestic forest dwellers have been designated as Critically Endangered on the IUCN Red List, making the Sumatran tiger one of the most endangered tiger subspecies on the planet. This is a rating reserved for animals that face an extremely high risk of extinction in the wild.

Latest surveys have indicated that there may now be as few as 300 existing in the wild. Kerinci Seblat National Park is one of the last places on Earth where they can still be found.

Today, around 170 tigers live in and around Kerinci Seblat National Park – the largest known population of tigers anywhere in Sumatra. Since 2007, the number of tigers in the park has stabilised - largely thanks to the vital work of

MEET YOUR MAKER

AIXSPONZA

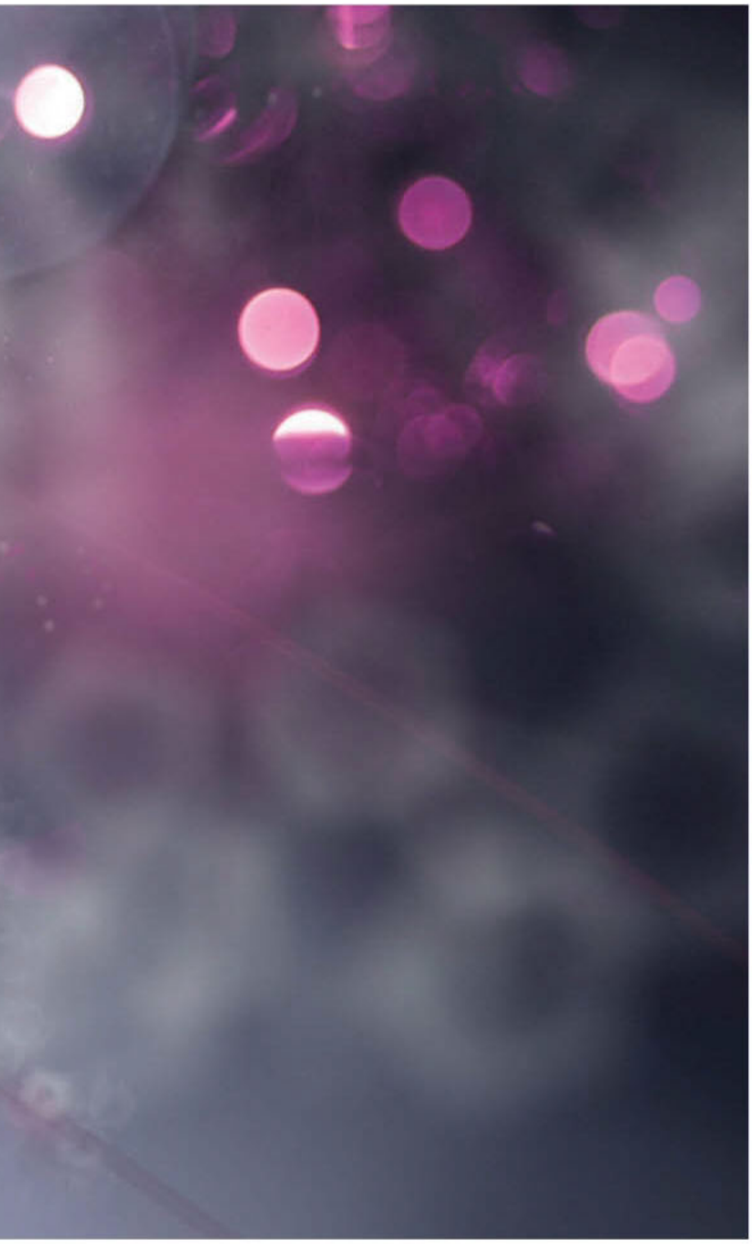
What did the last common ancestor of all life look like? **Michael Le Page** delves into the primordial soup

IN 1859, when Charles Darwin published *On The Origin of Species*, he dedicated an entire chapter to the problem of missing "intermediate links" – transitional forms that bridged the evolutionary gaps between closely related species. If his theory was correct, the fossil record should be full of them. Where were they?

At the time it was a real problem, as few such fossils had been found. Then came the spectacular discovery, in 1861, of *Archaeopteryx*, with the wings and feathers of a bird and the teeth and tail of a dinosaur.

Since then we have discovered a multitude of intermediate links: fish that could crawl, lizards with mammal-like jaws, whales with legs, giraffes with short necks and many others (see "Find the gaps", page 54). But there's one we are unlikely ever to find: the link between the earliest proto-life and life as we know it, also known as the last universal common ancestor, or LUCA.

LUCA lived around 4 billion years ago – a tiny, fragile life form that is the direct ancestor of every single living thing, from aardvarks to zebras. It wasn't the very first



life: thousands, if not millions, of years of evolutionary experimentation preceded it. But understanding LUCA would give us our best view yet of the origin of life.

We already know a surprising amount. Although any traces LUCA left in rocks were probably obliterated aeons ago, something far more revealing survives inside today's living cells: a biological operating system that is common to all life and must have been shared by LUCA too.

Many features of LUCA, though, have remained enigmatic, even paradoxical. But new work on a leading hypothesis for the origin of life might have solved many of the mysteries. It paints a detailed picture of where our earliest ancestor lived, how it lived and what it was like. Prepare to meet your maker.

Darwin himself was among the first scientists to speculate on how life originated: he envisaged a "warm little pond, with all sorts of ammonia and phosphoric salts, lights, heat, electricity, etc present". We will probably never know exactly how LUCA came to be, but we can make educated guesses by looking at some of the features of today's living systems.

These tell us much about what LUCA was like. We know it used DNA to store recipes for proteins, for instance. We even know what many of those recipes were, because many vital proteins found in all cells today must have come from LUCA. And from the nature of these proteins, it is clear that LUCA used an energy-rich molecule called ATP to fuel cellular processes, just as our cells do.

How did LUCA make its ATP? Anyone designing life from scratch would probably make ATP using chemical reactions inside the cell. But that's not how it is done. Instead, energy from food or sunlight is used to power a protein "pump" that shunts hydrogen ions – protons – out of the cell. This creates a difference in proton concentration, or a gradient, across the cell membrane. Protons then flow back into the cell through another protein embedded in the membrane, which uses the energy to produce ATP.

Think of a sink

To understand it in energy terms, think of a double kitchen sink. The small sink represents the inside of the cell and the large one the outside world. Start by filling the large sink with water, leaving the small one empty. The difference in water levels is a potential source of energy: drill a hole in the divider and water will flow into the small sink. The flow could be used to turn a tiny turbine – which is essentially what the ATP-making protein is, a turbine turned by protons and other positive ions (see diagram, page 8).

This process is so convoluted that when biochemist Peter Mitchell proposed it in 1961 it was dismissed as nonsense. But it has turned out to be common to all life, so most biologists think it must be how LUCA made ATP.

Exploiting a proton gradient requires a membrane that is impermeable to protons – they should only be able to flow in through the turbine. So it's assumed that LUCA had an impermeable membrane. But there is no evidence that this is the case. In fact, the nature of LUCA's membrane is an enigma.

To understand why, we have to backtrack to the 1970s, when it was thought that life could be divided into two great "empires". In one were animals, plants and fungi, and in the other the much simpler bacteria. Then microbiologist Carl Woese discovered that the bacterial empire actually contained two radically different types of life. A third "domain", now known as archaea, had been hiding in plain sight.

Archaea often look like bacteria, and are ›

"The building blocks of life would have formed spontaneously within the vents"

similar in many ways – as you would expect given that both evolved from LUCA, probably quite soon after it existed. There are also some fundamental differences between them. One is their membranes.

Both bacteria and archaea have membranes made of water-repellent fatty molecules. Simple fatty molecules tend to flip around, making the membrane leaky, so both bacteria and archaea tacked on a water-loving phosphate group to stabilise the molecules and make their membranes impermeable. They took very different routes, though. Bacterial membranes are made of fatty acids bound to the phosphate group while archaeal membranes are made of isoprenes bonded to phosphate in a different way. This suggests that their membranes evolved independently.

This leads to something of a paradox: if LUCA already had an impermeable membrane for exploiting proton gradients, why would its descendants have independently evolved two different kinds of impermeable membrane?

Nick Lane of University College London, a biochemist and award-winning science writer, has come up with a startling answer that challenges many widely held ideas. Far from being impermeable, LUCA's membrane was leaky. In fact, he argues, it had to be leaky.

Lane starts from the assumption that life originated on the sea floor at places called alkaline hydrothermal vents. This was proposed in 1989 by Michael Russell of NASA. Its proponents, including Lane and William Martin of the University of Dusseldorf in Germany, have argued that it alone can explain why life uses proton gradients to generate ATP. Now, says Lane, it can also explain another of life's key features: the membranes of archaea and bacteria.

Distinct from the better known black smokers, alkaline hydrothermal vents are places where warm alkaline fluids, at temperatures of between 40 °C and 90 °C, well up through cracks in the sea floor. As the fluid hits the cold seawater, minerals precipitate out of solution, gradually forming rocky chimneys up to 60 metres tall, full of narrow channels and pores.

Building blocks of life

Alkaline vents were present in primordial seas too. Within these ancient vents, Lane, Russell and Martin think, the building blocks of life would have formed spontaneously. The walls would have been rich in iron and sulphide, for example, which can catalyse complex organic reactions. What's more, temperature gradients within the pores should have created high concentrations of organic compounds and favoured the formation of large molecules, including lipids – fat molecules – and RNA.

So it would have been a perfect setting for the RNA world widely thought to have been the first step towards life. This may have been where self-replicating sets of RNA and other molecules first emerged and began to evolve into cell-like organisms with simple membranes. These proto-life forms needed energy – and it was provided, Martin and Lane argue, by the natural proton gradient at the

NOWA

interface between the proton-poor alkaline vent fluid and the proton-rich seawater. This is the ultimate origin of the proton gradients that power life today.

The stage was now set for the evolution, via a series of gradual steps, of the turbine protein that straddles the membrane and produces ATP. This was a crucial step in early evolution, though the cells could only survive at the interface between vent fluids and seawater, where there was a gradient to exploit. Only later did they evolve the ability to generate their own gradient using proton pumps.

It is a neat hypothesis but as critics have pointed out, there is a big catch. Early cells that had the ATP turbine protein but not proton

Life powers up

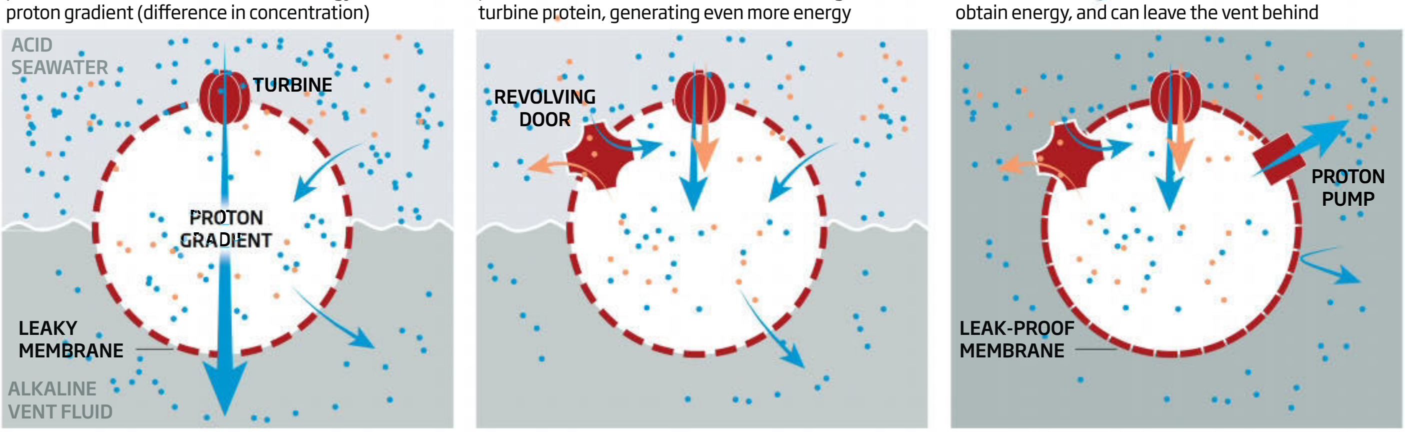
The earliest life on Earth could well have evolved at an undersea hydrothermal vent around 4 billion years ago. How did this cell get its energy, and how did it evolve to colonise the rest of the planet?

- PROTON
- SODIUM ION

The cell lives on the boundary between acid, proton-rich seawater, and alkaline vent fluid. It develops a protein that, like a turbine, extracts energy from the proton gradient (difference in concentration)

Later cells evolve a "revolving door" protein that effortlessly pumps sodium ions out while letting protons in. The sodium later re-enters through the turbine protein, generating even more energy

Eventually cells develop a dedicated proton pump and a leak-proof membrane. These cells can generate their own proton gradient across the membrane to obtain energy, and can leave the vent behind



Alkaline thermal vents on the sea floor: is this where life arose around 4 billion years ago?

> "Eventually, cells would have been able to break free altogether"

pumps would only have been able to generate a tiny amount of energy before the proton gradient collapsed. Without some means to shift protons out of the cell, the inside would quickly reach equilibrium with the outside.

To go back to the sink analogy, the water levels will rapidly equalise if water isn't being pumped out of the little sink. And so the hypothesis fails to explain how the universal ATP-making process arose. "It has worried me for some years," Lane says.

But you don't need a pump to restore the flow. All you have to do is to pull the plug out in the little sink. As it empties, the flow will resume. That is where the leaky membrane comes in.

Think of that primitive cell straddling the interface between seawater and vent fluid. One way to exploit the proton gradient is to have a leaky membrane. This would allow protons to flow continuously from seawater, through the cell, and back out into the vent fluid, without the gradient collapsing. As long as some of the incoming protons pass through ATP turbines, the cells have energy on tap.

Simple membranes made of fat molecules have just the required properties. In fact, fats spontaneously form cell-like structures that can grow and divide as more molecules are added. These properties mean they have long been of great interest to those exploring the origins of life. But the assumption was always that leak-proof membranes had to evolve before cells could exploit proton gradients. If Lane is correct, this is wrong.

Lane and Martin first sketched out the leaky membrane idea in 2012. Now Lane and his colleagues Andrew Pomiankowski and Victor Sojo have worked out a more detailed scenario and modelled it to see if it is energetically plausible. The results, published in 2014, confirm that leaky cells – unlike impermeable ones – could extract enough energy from a natural proton gradient.

Yet in solving one problem, the leaky membrane creates another. At some point cells broke their umbilical connection to the vents. To do so, they had to evolve energy-consuming proton pumps to generate their own gradients. But if you've got a leaky membrane, there's nothing to be gained from pumping protons. They just leak back in again.

Free energy

The obvious solution is for the membrane to evolve to be less leaky. But this doesn't work either, because it would have stopped protons flowing through and shut off the energy supply. Catch-22.

Or is it? According to Lane there is a way out. Modern cells have a third kind of protein in their membranes. These act like revolving doors (see diagram, left), swapping one ion for another across the membrane – a sodium ion for a proton, say – and they don't use any energy.

A revolving door like this could solve the leaky membrane conundrum. If early cells evolved a revolving door that exchanged sodium ions for protons, the game suddenly changes. Sodium ions cannot pass through leaky lipid membranes nearly as easily as protons, so the exchanger converts the natural proton gradient into a sodium ion gradient across the membrane. Crucially, sodium ions can re-enter the cell through the ATP turbine protein. So a cell with an exchanger will get more flow through its turbines and thus generate more ATP – up to 60 per cent more, according to the model.

Once a cell has revolving doors, evolving a proton pump becomes advantageous even with a leaky membrane: the more protons it pumps out, the more it can swap for sodium ions and the more ATP it can generate. As pumping increases, making the membrane less leaky becomes an advantage as well. That means natural selection would have driven the joint evolution of better pumps and less leaky membranes.

Cells could then survive in weaker gradients at the peripheries of vents. Eventually they would have been able to break free altogether and generate their own proton gradient across a non-leaky membrane. And this is what they did – not once but twice, giving rise to the bacteria and the archaea.

Other early-life researchers, though, will take some convincing. "I think this scenario is highly unlikely," says Jack Szostak of Harvard University, one of those who think that impermeable membranes evolved very early on. Cells with simple lipid membranes would leak not only ions but valuable metabolites, Szostak says.

How then did cells come to exploit proton gradients? That's not clear. Most researchers focus on very narrow features of early life, such as membranes or RNA. For now, only the alkaline vent scenario offers a broader picture, explaining not only where and how life came about, but why it has many of the peculiar features it does. "This paper is one of a series that deconstruct the organic soup hypothesis which has fooled us for almost 50 years now – that has always been blatantly anti-thermodynamic and hence basically out of the question," says Wolfgang Nitschke, a biochemist at the French national research agency in Marseille, who has studied the hydrothermal vent scenario.

This doesn't mean the vent scenario is right, but it does at least lead to predictions that can be put to the test.

For instance, can conditions like those in early alkaline vents really generate all the precursor molecules needed for life? Lane is trying to get funding to build a high-pressure reactor that would mimic the conditions at the deep-sea vents of 4 billion years ago.

In the meantime, consider this: we'll never know precisely what LUCA was like. But whatever it was, it lives on inside you. ■

GINA AND MATT

Dawn of the living

Life must have begun with a simple replicator – but what was it, and how did it work? Michael Marshall reports

4 BILLION years before present: the surface of a newly formed planet around a medium-sized star is beginning to cool down. It's a violent place, bombarded by meteorites and riven by volcanic eruptions, with an atmosphere full of toxic gases. But then something extraordinary happens. A molecule capable of replicating itself arises.

This was the dawn of evolution. Once the first self-replicating entities appeared, natural selection kicked in, favouring any offspring with variations that made them better at replicating themselves. Soon the first simple cells appeared. The rest is prehistory.

Billions of years later, some of the descendants of those first cells evolved into organisms intelligent enough to wonder what their very earliest ancestor was like. What molecule started it all?

Back in the 1960s, a few of those intelligent organisms began to suspect that the first self-replicating molecules were made of RNA, a close cousin of DNA. This idea has always had a problem, though – there was no known way by which RNA molecules could have formed on the primordial Earth. And if RNA molecules couldn't form spontaneously, how could self-replicating RNA molecules arise? Did some other replicator come first? If so, what was it? The answer is finally beginning to emerge.

When biologists first started to ponder how life arose, the question seemed baffling. In all organisms alive today, the hard work is done by proteins. Proteins can fold into a wild diversity of shapes, so they can do just about anything, including acting as enzymes, substances that catalyse a huge range of chemical reactions. However, the information needed to make proteins is stored in DNA molecules. You can't make new proteins without DNA, and you can't make new DNA without proteins. So which came first, proteins or DNA?

The discovery in the 1960s that RNA could fold like a protein, albeit not into such complex structures, suggested an answer. If RNA could catalyse reactions as well as storing information, some RNA molecules might be capable of making more RNA molecules. And if that was the case, RNA replicators would have had no need for proteins. They could do everything themselves.

It was an appealing idea, but at the time it was complete speculation. No one had shown that RNA could catalyse reactions like protein enzymes. It was not until 1982, after decades of searching, that an RNA enzyme was finally discovered. Thomas Cech of the University of Colorado in Boulder found it in *Tetrahymena thermophila*, a bizarre single-celled animal with seven sexes.

After that the floodgates opened. People discovered ever more RNA enzymes in living organisms and created new ones in their labs. RNA might be not be as good for storing information as DNA, being less stable, nor as versatile as proteins, but it was turning out to be a molecular jack of all trades. This was a huge boost to the idea that the first life consisted of RNA molecules that catalysed the production of more RNA molecules – "the RNA world", as Harvard chemist Walter Gilbert dubbed it three decades ago. ›

These RNA replicators may even have had sex. The RNA enzyme Cech discovered did not just catalyse any old reaction. It was a short section of RNA that could cut itself out of a longer chain. Reversing the reaction would add RNA to chains, meaning RNA replicators might have been able to swap bits with other RNA molecules. This ability would greatly accelerate evolution, because innovations made by separate lineages of replicators could be brought together in one lineage.

Evolving replicators

For many biologists the clincher came in 2000, when the structure of the protein-making factories in cells was worked out. This work confirmed that nestling at the heart of these factories is an RNA enzyme – and if proteins are made by RNA, surely RNA must have come first.

Still, some issues remained. For one thing, it was unclear whether RNA really was capable of replicating itself. Nowadays, DNA and RNA need the help of many proteins to copy themselves. If there ever was a self-replicator, it has long since disappeared. So biochemists set out to make one, taking random RNAs and evolving them for many generations to see what they came up with.

By 2001, this process had yielded an RNA enzyme called R18 that could stick 14 nucleotides – the building blocks of RNA and DNA – onto an existing RNA, using another RNA as a template. Any self-replicating RNA, however, needs to build RNAs that are at least as long as itself – and R18 doesn't come close.

A big advance came in 2013, when Philipp Holliger of the MRC Laboratory of Molecular Biology in Cambridge, UK, and colleagues unveiled an RNA enzyme called tC9Y. It is 202 nucleotides long, and reliably copies RNA sequences longer than itself, up to 206 letters long. To do this, tC9Y clamps onto the end of an RNA, attaches the correct nucleotide, then moves forward a step and adds another. "It blows my mind that you can do something so complex with such a simple molecule," Holliger says. Crucially, this enzyme does not yet copy itself and biologists have yet to pass this milestone. "There are various RNA systems that can assemble themselves from prefabricated pieces, but I would not call this self-replication, rather self-assembly," says Holliger.

There is another sticking point: where did the energy to drive this activity come from? There must have been some kind of metabolic process going on – but RNA does not look up to the job of running a full-blown metabolism.

"There's been a nagging issue of whether RNA can do all the chemistry," says Adrian Ferré-D'Amaré of the National Heart, Lung and Blood Institute in Bethesda, Maryland. RNA has only a few chemically active "functional groups", which limit it to catalysing just a few types of chemical reaction.

Functional groups are like tools – the more kinds you have, the more things you can do. Proteins have many more functional groups than RNAs. However, there is a way to make a single tool much more versatile: attach different bits to it, like those screwdrivers that come with interchangeable heads. The chemical equivalents are small helper molecules known as cofactors.

Proteins use cofactors to extend even further the range of reactions they can control. Without cofactors, life as we know it couldn't exist, Ferré-D'Amaré says. And it turns out that RNA enzymes can use cofactors too.

In 2003, Hiroaki Suga, now at the University of Tokyo, Japan, created an RNA enzyme that could oxidise alcohol, with help from a cofactor called NAD+ which is used by many protein enzymes. Months later, Ronald Breaker of Yale University found that a natural RNA enzyme, called glmS, also uses a cofactor.

Many bacteria use glmS, says Ferré-D'Amaré, so either it is ancient or RNA enzymes that use cofactors evolve easily. Either way, it looks as if RNA molecules would have been capable of carrying out the range of the reactions needed to produce energy.

So the evidence that there was once an RNA world is growing ever more convincing. Only a few dissenters remain. "The naysayers about the RNA world have lost a lot of ground," says Donna Blackmond of the Scripps Research Institute in La Jolla, California. But there is still one huge and obvious problem: where did the RNA come from in the first place?

RNA molecules are strings of nucleotides, which in turn are made of a sugar with a base and a phosphate attached. In living cells, numerous enzymes are involved in producing nucleotides and joining them together, but of course the primordial planet had no such enzymes. There was clay, though. In 1996, biochemist Leslie Orgel showed that when "activated" nucleotides – those with an extra bit tacked on to the phosphate – were added to a kind of volcanic clay, RNA molecules up to 55 nucleotides long formed. With ordinary

RODD HALSTEAD/GETTY

The first "cells" may have been water pockets in ice

XUAN CHE/GETTY

Darwin envisaged life beginning in a "warm little pond"

"It blows my mind that you can do something so complex with such a simple molecule"

nucleotides the formation of large RNA molecules would be energetically unfavourable, but the activated ones provide the energy needed to drive the reaction.

This suggests that if there were plenty of activated nucleotides on the early Earth, large RNA molecules would form spontaneously. What's more, experiments simulating conditions on the early Earth and on asteroids show that sugars, bases and phosphates would arise naturally too. It's putting the nucleotides together that is the hard bit; there does not seem to be any way to join the components without specialised enzymes. Because of the shapes of the molecules, it is almost impossible for the sugar to join to a base, and even when it does happen, the combined molecule quickly breaks apart.

This apparently insurmountable difficulty led many biologists to suspect to RNA was not the first replicator after all. Many began exploring the possibility that the RNA world was preceded by a TNA world, or a PNA world, or perhaps an ANA world. These are all molecules similar to RNA but whose basic units are thought to have been much more likely to form spontaneously. The big problem with this idea is that if life did begin this way, no evidence of it remains. "You don't see a smoking gun," says Gerald Joyce, also of the Scripps Research Institute.

In the meantime John Sutherland, at the MRC Laboratory of Molecular Biology, has been doggedly trying to solve the nucleotide problem. He realised that researchers might have been going about it the wrong way. "In each nucleotide, you see a sugar, a base and a phosphate group," he says. "So you assume you need to make those building blocks first and then stick them together… and it doesn't work."

Instead he wondered whether simpler molecules might assemble into a nucleotide without ever becoming sugars or bases. In 2009, he proved it was possible. He took half a sugar and half a base, and stuck them together – forming the crucial sugar-base link that everyone had struggled with. Then he bolted on the rest of the sugar and base. Sutherland stuck on the phosphate last, though he found that it needed to be present in the mixture for the earlier reactions to work. "Sutherland had a real breakthrough," Holliger says. "Everyone else was barking up the wrong tree."

Goldilocks chemistry

Sutherland was being deliberately messy by including the phosphate from the start, but it gave the best results. That's encouraging: the primordial Earth was a messy place and it may have been ideal for making nucleotides. At that time, Sutherland suspected there was a "Goldilocks chemistry" – not too simple, not too complex – that would produce many key compounds from the same melting pot. In 2015 he proved it, showing that precursors to ribonucleotides, lipids and amino acids could be created out of two simple compounds abundant on early Earth – hydrogen cyanide and hydrogen sulphide – plus UV light.

The issue isn't entirely solved yet. RNA has four different nucleotides, and so far Sutherland has only produced two of them. However, he says he is "closing in" on the other two. If he succeeds, it will show that the spontaneous formation of an RNA replicator is not so improbable after all, and that the first replicator was most likely made of RNA.

Many questions remain, of course. What was the first life like? How did the transition to DNA and proteins, and the development of the genetic code, occur? We may never know for sure but many promising avenues are being explored. Most biologists think there must have been something like a cell right from the start, to contain the replicator and keep its component parts together. That way, individuals could compete for resources and evolve in different ways.

Jack Szostak of Harvard University has shown that the same clay that produces RNA chains also encourages the formation of membrane-bound sacs rather like cells that enclose cells. He has grown "proto-cells" that can carry and replicate RNA and even divide without modern cellular machinery.

Another idea is that life began in alkaline hydrothermal vents on the sea floor (see "Meet your maker", page 6). Not only are these vents laced with pores and bubbles, but they also provide the same kind of electrochemical gradient that drives energy production in cells to this day. Conditions may have been ideal for producing long RNA chains.

Holliger has another idea: maybe it all happened in ice. At the time life began, the sun was 30 per cent dimmer than today. The planet would have frozen over if the atmosphere hadn't been full of greenhouse gases, and there may well have been ice towards the poles. Cold RNA lasts longer, and ice has many other benefits. When water laced with RNA and other chemicals is cooled, some of it freezes while the rest becomes a concentrated brine running around the ice crystals. "You get little pockets within the ice," Holliger says. Interestingly, the R18 and tC9Y RNA enzymes can work better in ice than at room temperature – tC9Y can even synthesise RNA at temperatures as low as -19 °C. And in 2015 Holliger and colleagues demonstrated that freeze-thaw cycles allow complex RNA molecules to spontaneously assemble from simpler ones.

Right now, there's no way to choose between these options. No fossilised vestiges remain of the first replicators as far as we know. But we can try recreating the RNA world to demonstrate how it might have arisen. One day soon, Sutherland says, someone will fill a container with a mix of primordial chemicals, keep it under the right conditions, and watch life emerge. "That experiment will be done." ■

ANDRIO ABERO/DUTCHUNCLE.CO.UK

In theory, life ought to arise wherever conditions are right. But that doesn't mean the universe is teeming with creatures like us, says **Nick Lane**

Life: Inevitable, fluke or both?

FOR four years, the Kepler space telescope scoured the sky for Earth-like planets around other stars. When its mission ended in August 2013, it had found so many that NASA came to a startling conclusion: our galaxy is teeming with planets capable of hosting life. There are perhaps 40 billion of them, 11 billion of which are small rocky worlds orbiting sunlike stars at a distance where liquid water may exist.

These discoveries are bringing an old paradox back into focus. As physicist Enrico Fermi asked in 1950, if there are many suitable homes for life out there and alien life forms are common, where are they all? More than half a century of searching for extraterrestrial intelligence has so far come up empty-handed.

Of course, the universe is a very big place. Even Frank Drake's famously optimistic "equation" for life's probability suggests that we will be lucky to stumble across intelligent aliens: they may be out there, but we'll never know it. That answer satisfies no one, however.

There are deeper explanations. Perhaps alien civilisations appear and disappear in a galactic blink of an eye, destroying themselves long before they become capable of colonising new planets. Or maybe life very rarely gets started even when conditions are perfect.

If we cannot answer these kinds of questions by looking out, might it be possible to get some clues by looking in? Life arose only once on Earth, and if a sample of one were all we had to go on, no grand conclusions could be drawn. But there is more than that. Looking at a vital ingredient for life – energy – suggests that simple life is common throughout the universe, but it does not inevitably evolve into more complex forms such as animals. I might be wrong, but if I'm right, the immense delay between life first appearing on Earth and the emergence of complex life points to ›

another, very different explanation for why we have yet to discover aliens.

Living things consume an extraordinary amount of energy, just to go on living. The food we eat gets turned into the fuel that powers all living cells, called ATP. This fuel is continually recycled: over the course of a day, humans each churn through 70 to 100 kilograms of the stuff. This huge quantity of fuel is made by enzymes, biological catalysts fine-tuned over aeons to extract every last joule of usable energy from reactions.

The enzymes that powered the first life cannot have been as efficient, and the first cells must have needed a lot more energy to grow and divide – probably thousands or millions of times as much energy as modern cells. The same must be true throughout the universe.

This phenomenal energy requirement is often left out of considerations of life's origin. What could the primordial energy source have been here on Earth? Old ideas of lightning or ultraviolet radiation just don't pass muster. Aside from the fact that no living cells obtain their energy this way, there is nothing to focus the energy in one place. The first life could not go looking for energy, so it must have arisen where energy was plentiful.

Today, most life ultimately gets its energy from the sun via photosynthesis by plants. But photosynthesis is an enormously complex process and probably didn't power the first life. So what did?

Reconstructing the history of life by comparing the genomes of simple cells is fraught with problems. Nevertheless, such studies all point in the same direction. The earliest cells seem to have gained their energy and carbon from the gases hydrogen and carbon dioxide. The reaction of H_2 with CO_2 produces organic molecules directly, and releases energy. That is important, because it is not enough to form simple molecules: it takes buckets of energy to join them up into the long chains that are the building blocks of life.

A second clue to how the first life got its energy comes from the energy-harvesting mechanism found in all known life forms. This mechanism was so unexpected that there were two decades of heated altercations after it was proposed by British biochemist Peter Mitchell in 1961.

Universal force field

Mitchell suggested that cells are powered not by chemical reactions, but by a kind of electricity, specifically by a difference in the concentration of protons (the charged nuclei of hydrogen atoms) across a membrane. Because protons have a positive charge, the concentration difference produces an electrical potential difference between the two sides of the membrane of about 150 millivolts. It might not sound like much, but because it operates over only 5 millionths of a millimetre, the field strength over that tiny distance is enormous, around 30 million volts per metre. That's equivalent to a bolt of lightning.

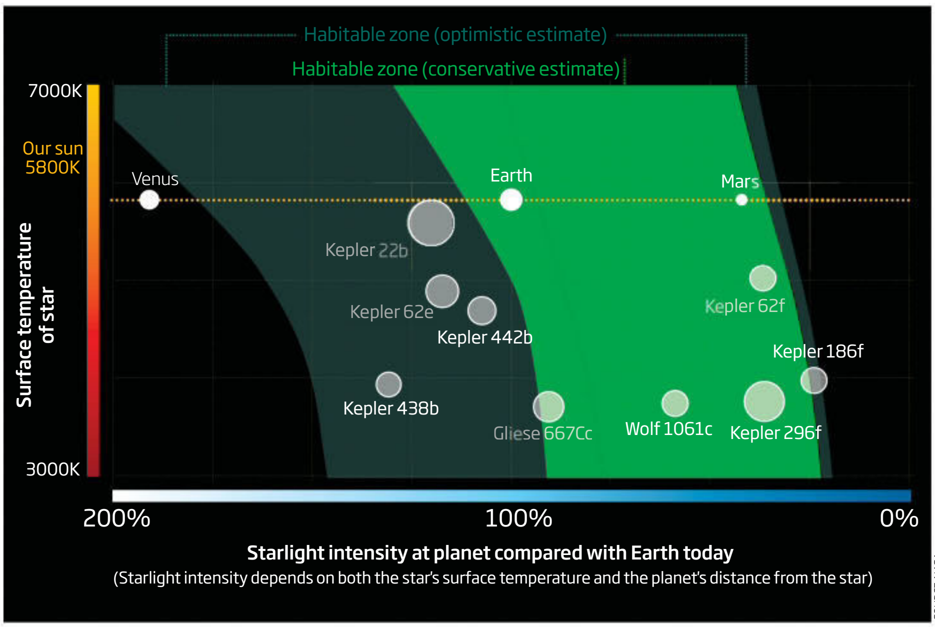
Mitchell called this electrical driving force the proton-motive force. It sounds like a term from *Star Wars*, and that's not inappropriate. Essentially, all cells are powered by a force field as universal to life on Earth as the genetic code. This tremendous electrical potential can be tapped directly, to drive the motion of flagella, for instance, or harnessed to make the energy-rich fuel ATP.

However, the way in which this force field is generated and tapped is extremely complex. The enzyme that makes ATP is a rotating motor powered by the inward flow of protons. Another protein that helps to generate the membrane potential, NADH dehydrogenase, is like a steam engine, with a moving piston for pumping out protons. These amazing nanoscopic machines must be the product of prolonged natural selection. They could not have powered life from the beginning, which leaves us with a paradox.

Life guzzles energy, and inefficient primordial cells must have required much more energy, not less. These vast amounts of energy are most likely to have derived from a

The habitable zone

A star's habitable zone is the region around it in which an Earth-like planet can have liquid water. The search for extrasolar planets is in its infancy but has already found a number in the habitable zones of their stars



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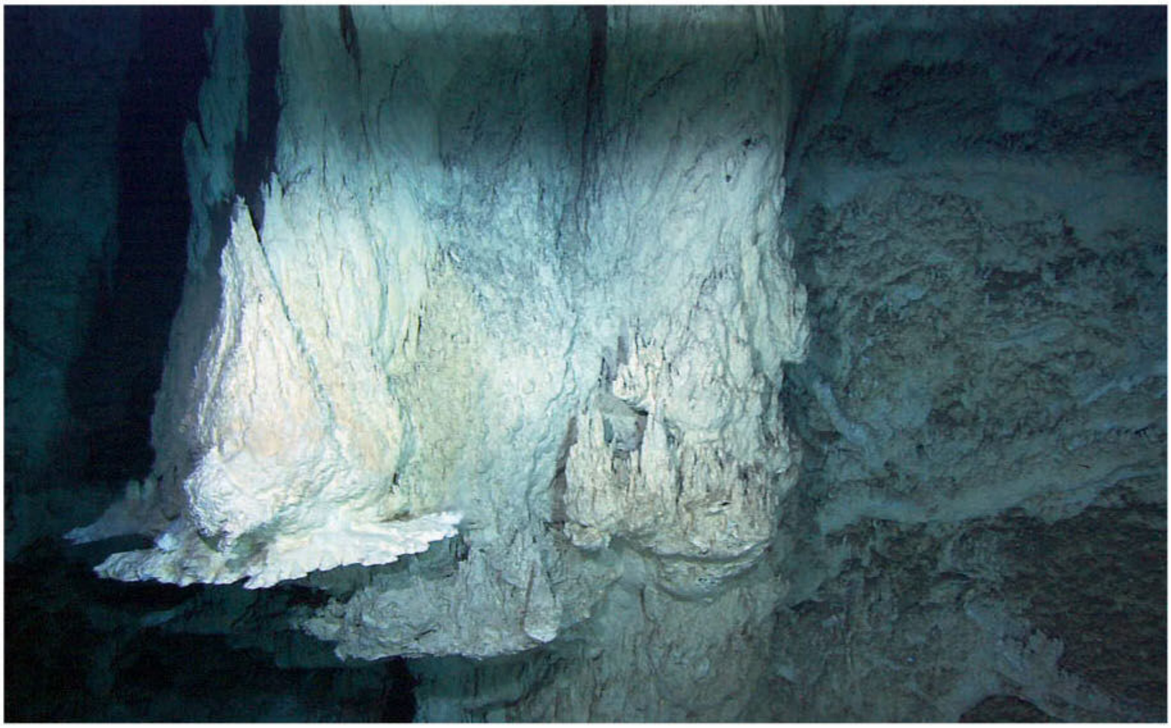

D. KELLEY/UNIVERSITY OF WASHINGTON

Alkaline thermal vents may have incubated the first life

proton gradient, because the universality of this mechanism means it evolved early on. But how did early life manage something that today requires very sophisticated machinery?

There is a simple way to get huge amounts of energy this way. What's more, the context makes me think that it really wasn't that difficult for life to arise in the first place.

The answer I favour was proposed 20 years ago by the geologist Michael Russell, now at NASA's Jet Propulsion Laboratory in Pasadena, California, who had been studying deep-sea hydrothermal vents. Say "deep-sea vent" and many people think of dramatic black smokers surrounded by giant tube worms. Russell had something much more modest in mind: alkaline hydrothermal vents. These are not volcanic at all, and don't smoke. They are formed as seawater percolates down into the electron-dense rocks found in the Earth's mantle, such as the iron-magnesium mineral olivine.

Olivine and water react to form serpentinite in a process that expands and cracks the rock, allowing in more water and perpetuating the reaction. Serpentinisation produces alkaline fluids rich in hydrogen gas, and the heat it releases drives these fluids back up to the ocean floor. When they come into contact with cooler ocean waters, the minerals precipitate out, forming towering vents up to 60 metres tall. Such vents, Russell realised, provide everything needed to incubate life. Or rather they did, 4 billion years ago.

Back then, there was very little, if any, oxygen, so the oceans were rich in dissolved iron. There was probably a lot more CO_2 than there is today, which meant that the oceans were mildly acidic – that is, they had an excess of protons.

Just think what happens in a situation like this. Inside the porous vents, there are tiny, interconnected cell-like spaces enclosed by flimsy mineral walls. These walls contain the same catalysts – notably various iron, nickel and molybdenum sulphides – used by cells today (albeit embedded in proteins) to catalyse the conversion of CO_2 into organic molecules.

Fluids rich in hydrogen percolate through this labyrinth of catalytic micropores. Normally, it is hard to get CO_2 and H_2 to react: efforts to capture CO_2 to reduce global warming face exactly this problem. Catalysts alone may not be enough. But living cells don't capture carbon using catalysts alone – they use proton gradients to drive the reaction. And between a vent's alkaline fluids and acidic water there is a natural proton gradient.

Could this natural proton-motive force have driven the formation of organic molecules? I'm working on exactly that question. It is too early to say for sure, but the early signs are that the answer is yes.

What would that solve? A great deal. Once the barrier to the reaction between CO_2 and H_2 is down, the reaction can proceed apace. Remarkably, under conditions typical of alkaline hydrothermal vents, the combining of H_2 and CO_2 to produce the molecules found in living cells – amino acids, lipids, sugars and nucleobases – actually releases energy.

That means that far from being some mysterious exception to the second law of thermodynamics, from this point of view, life is in fact driven by it. It is an inevitable consequence of a planetary imbalance, in which electron-rich rocks are separated from electron-poor, acidic oceans by a thin crust, perforated by vent systems that focus this electrochemical driving force into cell-like systems. The planet can be seen as a giant battery; the cell is a tiny battery built on basically the same principles.

I'm the first to admit that there are many gaps to fill in, many steps between an electrochemical reactor that produces organic molecules and a living, breathing cell. But consider the bigger picture for a moment. The origin of life needs a very short ›

"EXISTING LIFE FORMS GUZZLE ENERGY, AND INEFFICIENT PRIMORDIAL CELLS MUST HAVE REQUIRED MUCH MORE ENERGY. HOW DID THEY MANAGE?"

shopping list: rock, water and CO_2.

Water and olivine are among the most abundant substances in the universe. Many planetary atmospheres in the solar system are rich in CO_2, suggesting that it is common too. Serpentinisation is a spontaneous reaction, and should happen on a large scale on any wet, rocky planet. From this perspective, the universe should be teeming with simple cells – life may indeed be inevitable whenever the conditions are right. It's hardly surprising that life on Earth seems to have begun almost as soon as it could.

Then what happens? It is generally assumed that once simple life has emerged, it gradually evolves into more complex forms, given the right conditions. But that's not what happened on Earth. After simple cells first appeared, there was an extraordinarily long delay – nearly half the lifetime of the planet – before complex ones evolved. What's more, simple cells gave rise to complex ones just once in 4 billion years of evolution: a shockingly rare anomaly, suggestive of a freak accident.

If simple cells had slowly evolved into more complex ones over billions of years, all kinds of intermediate cells would have existed and some still should. But there are none. Instead, there is a great gulf. On the one hand, there are the prokaryotes (bacteria and archaea), tiny in both their cell volume and genome size. They are streamlined by selection, pared down to a minimum: fighter jets among cells. On the other, there are the vast and unwieldy eukaryotic cells, more like aircraft carriers than fighter jets. A typical single-celled eukaryote is about 15,000 times larger than a bacterium, with a genome to match.

All the complex life on Earth – animals, plants, fungi and so on – are eukaryotes, and they all evolved from the same ancestor. So without the one-off event that produced the ancestor of eukaryotic cells, there would have been no plants and fish, no dinosaurs and apes. Simple cells just don't have the right cellular architecture to evolve into more complex forms.

Why not? I recently explored this issue with the pioneering cell biologist Bill Martin of the University of Düsseldorf, Germany. Drawing on data about the metabolic rates and genome sizes of various cells, we calculated how much energy would be available to simple cells as they grew bigger.

What we discovered is that there is an extraordinary energetic penalty for growing larger. If you were to expand a bacterium up to eukaryotic proportions, it would have tens of thousands of times less energy available per gene than an equivalent eukaryote. And cells need lots of energy per gene, because making a protein from a gene is an energy-intensive process. Most of a cell's energy goes into making proteins.

At first sight, the idea that bacteria have nothing to gain by growing larger would seem to be undermined by the fact that there are some giant bacteria bigger than many complex cells, notably *Epulopiscium*, which thrives in the gut of the surgeonfish. Yet *Epulopiscium* has up to 200,000 copies of its complete genome. Taking all these multiple genomes into consideration, the energy available for each copy of any gene is almost exactly the same as for normal bacteria, despite the vast total amount of DNA. They are perhaps best seen as consortia of cells that have fused together into one, rather than as giant cells.

So why do giant bacteria need so many copies of their genome? Recall that cells harvest energy from the force field across their membranes, and that this membrane potential equates to a bolt of lightning. Cells get it wrong at their peril. If they lose control of the membrane potential, they die. Nearly 20 years ago, biochemist John Allen, then at Queen Mary, University of London, suggested that genomes are essential for controlling the membrane potential, by controlling protein production. These genomes need to be near the membrane they control so they can respond swiftly to local changes in conditions. Allen and others have amassed a good deal of evidence that this is true for eukaryotes, and there are good reasons to think it applies to simple cells, too.

So the problem that simple cells face is this. To grow larger and more complex, they have to generate more energy. The only way they

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"WHEN WE LOOK AT WHAT BACTERIA NEED TO BECOME MORE COMPLEX, WE SEE THEY OCCUPY A DEEP CANYON IN THE ENERGY LANDSCAPE"

can do this is to expand the area of the membrane they use to harvest energy. To maintain control of the membrane potential as the area of the membrane expands, though, they have to make extra copies of their entire genome – which means they don't actually gain any energy per gene copy.

Put another way, the more genes that simple cells acquire, the less they can do with them. And a genome full of genes that can't be used is no advantage. This is a tremendous barrier to growing more complex, because making a fish or a tree requires thousands more genes than bacteria possess.

So how did eukaryotes get around this problem? By acquiring mitochondria.

About 2 billion years ago, one simple cell somehow ended up inside another. The identity of the host cell isn't clear, but we know it acquired a bacterium, which began to divide within it. These cells within cells competed for succession; those that replicated fastest, without losing their capacity to generate energy, were likely to be better represented in the next generation.

And so on, generation after generation, these "endosymbiotic" bacteria evolved into tiny power generators, containing both the membrane needed to make ATP and the genome needed to control membrane potential. Crucially, though, along the way they were stripped down to a bare minimum. Anything unnecessary has gone, in true bacterial style. Mitochondria originally had a genome of perhaps 3000 genes; nowadays they have just 40 or so genes left.

For the host cell, it was a different matter. As the mitochondrial genome shrank, the amount of energy available per host-gene copy increased and its genome could expand. Awash in ATP, served by squadrons of mitochondria, it was free to accumulate DNA and grow larger. You can think of mitochondria as a fleet of helicopters that "carry" the DNA in the nucleus of the cell. As mitochondrial genomes were stripped of their own unnecessary DNA, they became lighter and could each lift a heavier load, allowing the nuclear genome to grow ever larger.

These huge genomes provided the genetic raw material that led to the evolution of complex life. Mitochondria did not prescribe complexity, but they permitted it. It's hard to imagine any other way of getting around the energy problem – and we know it happened just once on Earth because all eukaryotes descend from a common ancestor.

Freak of nature

The emergence of complex life, then, seems to hinge on a single fluke event – the acquisition of one simple cell by another. Such associations may be common among complex cells, but they are extremely rare in simple ones. And the outcome was by no means certain: the two intimate partners went through a lot of difficult co-adaptation before their descendants could flourish.

This does not bode well for the prospects of finding intelligent aliens. It means there is no inevitable evolutionary trajectory from simple to complex life. Never-ending natural selection, operating on infinite populations of bacteria over billions of years, may never give rise to complexity. Bacteria simply do not have the right architecture. They are not energetically limited as they are – the problem only becomes visible when we look at what it would take for their volume and genome size to expand. Only then can we see that bacteria occupy a deep canyon in an energy landscape, from which they are unable to escape.

So what chance life? It would be surprising if simple life were not common throughout the universe. Simple cells are built from the most ubiquitous of materials – water, rock and CO_2 – and they are thermodynamically close to inevitable. Their early appearance on Earth, far from being a statistical quirk, is exactly what we would expect.

The optimistic assumption of the Drake equation was that on planets where life emerged, 1 per cent gave rise to intelligent life. But if I'm right, complex life is not at all inevitable. It arose here just once in 4 billion years thanks to a rare, random event. There's every reason to think that a similar freak accident would be needed anywhere else in the universe too. Nothing else could break through the energetic barrier to complexity.

This line of reasoning suggests that while Earth-like planets may teem with life, very few ever give rise to complex cells. That means there are very few opportunities for plants and animals to evolve, let alone intelligent life. So even if we discover that simple cells evolved on Mars, too, it won't tell us much about how common animal life is elsewhere in the universe.

All this might help to explain why we've never found any sign of aliens. Of course, some of the other explanations that have been proposed, such as life on other planets usually being wiped out by catastrophic events such as gamma-ray bursts long before smart aliens get a chance to evolve, could well be true too. If so, there may be very few other intelligent beings in the galaxy.

Then, again, perhaps some just happen to live in our neighbourhood. If we do ever meet them, there's one thing I would bet on: they will have mitochondria too. ■

Under a cold sun

How did life on Earth get started, when our young planet should have been frozen and inhospitable? **Stuart Clark** investigates

WHY are we here? As questions go, it's a big 'un, beloved of philosophers and theologists in a navel-gazing, hand-wringing sort of way. Scientists often find themselves raising an objection before the others even start: we probably shouldn't be here to ask the question in the first place.

The existence of life on Earth seems to have been the product of many lucky turns of events. Take the sun's early history. According to everything we know about how stars like it develop, it should have been born feebly dim, only gradually warming to its present level. Earth, born with the sun 4.5 billion years ago, should have spent its first 2 billion years or so as a frozen ball of ice, devoid of life.

Yet in rocks laid down during this time we find sediments clearly deposited in aquatic environments, and ample fossil evidence of bacteria that indicate our planet was already a clement, inhabited world, perhaps within a billion years or so from the off. This mismatch, known as the faint young sun paradox, has many potential solutions. None quite has the ring of truth. But as suggestions accumulate and are discarded, one conclusion seems ever harder to ignore: we are even luckier to be here than we thought.

The faint young sun paradox has its origins in the 1960s, when astrophysicists ran the first crude computer simulations of how changes in chemical composition affect the luminosity and heat output of stars such as our sun. The results were clear: the greater abundance of hydrogen in the early sun's core would have given it a higher internal pressure, expanding the star's nuclear heart and lowering its temperature. As a result, the sun's output in its early years was 25 to 30 per cent lower than it is today. That translates into an average surface temperature of the early Earth some 20 degrees cooler –

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about 10 degrees below water's freezing point.

Yet records of liquid water on Earth go back almost as far as the planet itself. Deposits of the mineral zircon in rocks from Jack Hills in Western Australia have been dated to 4.4 billion years ago, and contain oxygen isotopes that point to their having formed in a watery environment. In the same region there are fossil stromatolites, layered structures formed in shallow water by microbial communities, thought to date to 3.5 billion years ago.

"This clearly tells us that simple models for planetary habitability are wrong," says David Minton, a planetary scientist at Purdue University in West Lafayette, Indiana. "There was life on Earth when it should have been a frozen wasteland." Minton was one of a few dozen astrophysicists and geophysicists who met in Baltimore, Maryland, in 2012 to discuss ways out of this bind. "It turned out that there were almost as many potential solutions as there were participants," he says.

An early proposal is still the most popular: that some greenhouse gas allowed the early Earth's atmosphere to trap more of the weak sun's rays. The suggestion was first made in 1972 in *Science* by astronomers Carl Sagan and George Mullen. But as they discovered, finding the right gas is tricky.

Correct cocktails

Carbon dioxide seems unlikely to be the sole culprit. CO_2 enters soil either in raindrops or through direct diffusion, and drives chemical weathering that is reflected in the mineral composition of rocks known as palaeosols. Studies of ancient palaeosols do suggest atmospheric CO_2 levels were higher back in the Archean era, which ran from 3.8 billion years ago to 2.5 billion years ago. But to keep the oceans at a surely liquid temperature of 5 degrees above freezing, they would need to be some 300 times the current amount – 10 times more than even the most generous palaeosol estimates.

James Kasting, a palaeoclimatologist at Penn State University in Philadelphia, still thinks a CO_2-based greenhouse effect is the solution, pointing to other evidence of its role in mediating Earth's temperature (see "Carbon control", page 23). "I pay attention to those estimates even if I don't completely agree with some them," he says. All that is needed is to find the correct cocktail of other gases that was mixed in with the CO_2.

Back in 1972, Sagan and Mullen suggested ammonia and methane. But ammonia is highly susceptible to ultraviolet light and, with no protective ozone layer around the early Earth, would have been destroyed easily even by the faint young sun's rays. Methane is a powerful greenhouse gas but above a certain ›

"Atmospheric composition, rotation, albedo, the effect of clouds could all be the answer – or they could be red herrings"

concentration forms an organic haze that absorbs sunlight, radiating it back into space. Too much methane cools a planet's surface instead of warming it – an effect astronomers have seen on Saturn's moon Titan.

Titan suggests other ways of making Earth's early atmosphere more of a comforting blanket. While at the University of Chicago in 2013, Robin Wordsworth and Raymond Pierrehumbert, investigated whether high levels of nitrogen and hydrogen, such as are found on Titan, can have a warming effect. While the answer is yes, there is no evidence that Earth's atmosphere was ever dense enough to hold the required quantities.

"It turns out that all the gases are more problematic than you hope," says Georg Feulner of the Potsdam Institute for Climate Impact Research in Germany. He believes one reason the paradox has yet to be resolved is that the computer models generally used to study ancient climates are too crude to provide meaningful results.

Relentless activity

The models are crude because they typically ignore factors such as Earth's rotation, which has slowed over the years owing to the effect of the moon's gravity. This slowing would have altered the pattern of heat transport from the equator to the poles, perhaps changing the extent of ice cover and so the amount of energy that was reflected straight back up into space rather than being absorbed by Earth.

This quantity, the albedo, is a general problem. "We know nothing at all about the albedo of the early Earth," says Kasting. Oceans tend to absorb more heat than land does, so the albedo will be affected by factors such as the arrangement of the continents. Thanks to Earth's relentless tectonic activity, this would have been very different in the distant past. Minik Rosing and his colleagues at the University of Copenhagen, Denmark, have even controversially argued that considerably reduced continental cover, plus chemical differences in cloud cover, would have reduced the albedo enough to explain the faint young sun paradox without the need to invoke higher levels of greenhouse gases at all.

All of these factors – atmospheric composition, rotation, albedo, the effect of clouds – could be the key to solving the paradox. Or they could be red herrings. We simply do not know. Feulner's own latest attempt at a more sophisticated climate model (albeit with a simplified atmosphere) suggests that previous studies have underestimated the cooling effects of faster rotation and ice cover, making the faint young sun paradox even more of a problem. However, other studies using sophisticated atmosphere models but without the important effects of ocean and sea-ice dynamics, did not find this.

A few years down the line, he hopes to bring together the teams working on simulations of the early Earth's climate to compare results. That way they can see which effects are a result of the theoretical assumptions that go into making individual models. Any warming effects that pop up in all models, regardless of the assumptions, stand a greater chance of being the key to the problem.

Meanwhile some geophysicists continue to cast a suspicious eye at the sun. Is it possible that astrophysicists have not got the workings of our star nailed down? "Every 10 years or so, someone proposes that the sun must have been more massive in the past," says Kasting. The excess would have to have been substantial – about 2.5 per cent, or 8250 Earth masses – to have made the sun shine brightly enough. Although the sun is constantly flinging particles into space, creating the solar wind, it currently takes 150 million years to lose the mass equivalent to a single Earth. That means the solar wind must have been stronger in the past – a great deal stronger. "That's a sustained mass loss which is at least 10 times larger than anything we infer through the observation of other stars," says Minton.

The book is not closed on all astronomical suggestions. Minton's own involves a game of planetary billiards, and is inspired by the work of Jacques Laskar of the Paris Observatory in France. In 2009, Laskar made headlines with a series of computer simulations that showed that the orbits of the solar system's inner planets are not necessarily stable over billions of years. In one particularly alarming scenario, the gravity of the outer solar system's giant, Jupiter, might destabilise Mercury's orbit, flinging it outwards and potentially causing collisions between it, Venus, Earth and Mars in about 3.5 billion years' time.

Orbital shift

Minton thinks what may be possible in the future could also be true of the past. He investigated what it would have taken for Earth to form closer to the sun and only move out to its present orbit later, neatly solving the faint young sun paradox. In work yet to be published, he has found that it would not have taken much. "You only need to change the orbit of Earth by a few per cent," he says. Even

Five ways to a warmer Earth

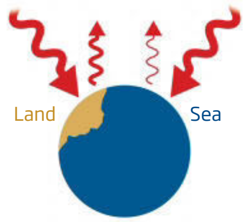
For its first two billion years or so the sun should not have been warm enough to make Earth hospitable to life. Many solutions have been proposed to this paradox - but all have their own problems

A HOTTER GREENHOUSE

A more powerful blanket of greenhouse gases around the early Earth trapped more heat

PROBLEM Which gases?

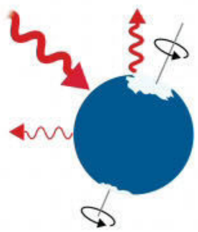
HIGHER ALBEDO



Land reflects more heat than ocean – so if the early Earth had more ocean cover it would have retained more heat

PROBLEM How do you test it?

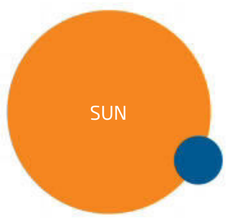
FASTER ROTATION



Earth's faster past spinning could have transferred heat to the poles more quickly than today, melting reflective ice there

PROBLEM Effect is too small on its own

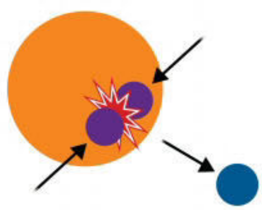
A BIGGER SUN



The early sun was more massive to compensate for its lower luminosity

PROBLEM Where did all that extra mass go?

PLANETARY BILLIARDS



A collision of two other planets nudged Earth out of a warm nursery closer to the sun

PROBLEM No evidence

so, such an orbital shift is something that is easier to make happen with a catastrophe, rather than gradually. The catastrophe Minton imagined was a collision between two planets about 2.5 billion years ago that created the present-day Venus. The resulting small change in the gravitational environment would have been enough to nudge Earth outwards to its present location, ensuring that as the sun warmed up, life on Earth did not roast.

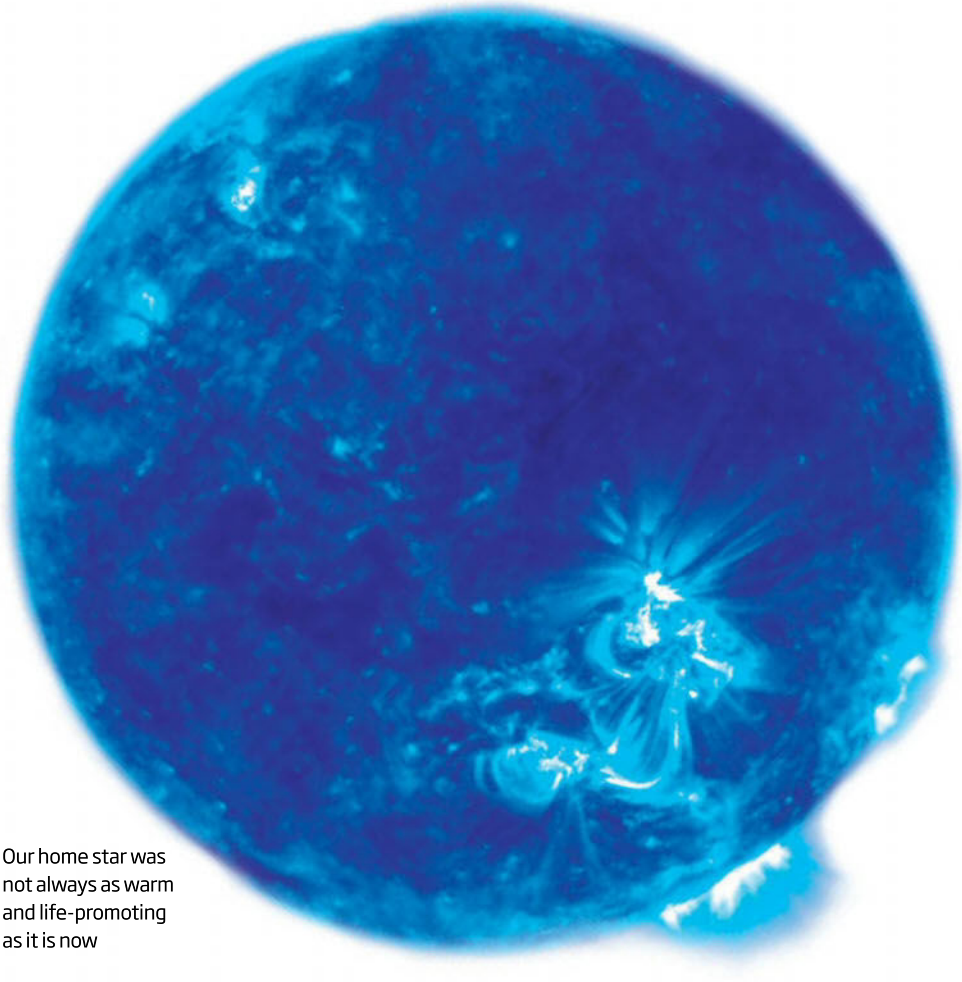
Even Minton admits the idea is a little wacky – and almost impossible to test. A planet's age can often be estimated by the density of craters on its face, but those on Venus are hidden well. A simple count of its craters suggests a figure of just 500 million to a billion years – far too young to be a plausible age under any scenario. Something must have happened to Venus's surface to smooth out earlier wrinkles. Until we work out what, we are at a loss to work out the planet's true age.

Kasting, too, is sceptical of Minton's idea, and invokes Occam's razor. "You should keep solutions simple," he says. Unfortunately, simple solutions are what we currently lack. Indeed, all the indications are that no single factor can explain away the faint young sun paradox. And that raises a wider question. If Earth's habitability is indeed a product of a finely tuned combination of events, how many other planets have been able to tread a similarly unlikely path?

Feulner shrugs off the question, saying we need to put our own house in order before going on to speculate about other worlds. "As our understanding of ancient climates is still so preliminary, I'd be happy to understand the solution to the faint young sun paradox first, and then wonder about the consequences."

Minton takes a different view. If there are many feasible solutions to the paradox – even if only one of them can be true for the Earth – others could be playing out on other planets around the galaxy. The many different ways to achieve habitability may overwhelm the implausibility of any single solution. "There may be so many complicating factors that the whole thing just opens up," he says. "Biospheres may be much more robust than we think, and planetary environments we currently consider to be utterly hostile could themselves be perfectly hospitable."

For those prone to loneliness and existential angst that is perhaps a comforting thought. Although it still doesn't answer the question: why *are* we here? ■



Our home star was not always as warm and life-promoting as it is now

RGB VENTURES/LLC DBA/SUPERSTOCK/ALAMY

Carbon control

All the evidence suggests that Earth's Archean era, which ended 2.5 billion years ago, was substantially warmer than models of the sun's early development allow (see main story), But there is no doubt as to how the era ended: our planet abruptly chilled into its first ice age. Known as the Huronian glaciation, this was one of the longest, most severe ice ages in Earth's history - and it took place just when the sun should have been reaching temperatures capable of turning our planet into a clement world. Why?

James Kasting of Penn State University in Philadelphia points to a possible culprit: life - in particular the oxygen given out by the first photosynthesising bacteria. Oxygen tears apart methane, a powerful greenhouse gas, to create carbon dioxide and water. "Before the rise of oxygen, methane was stable in the atmosphere for 10,000 years," he says. Afterwards, the average molecule lasted just a decade or so. Methane is a much more efficient greenhouse gas than the CO_2 created in this process, so Earth cooled.

But how then did our planet escape its ice age again? The answer probably lies in how atmospheric CO_2 dissolves in rainwater and enters soils, chemically weathering the existing rocks and building carbonate minerals that are eventually taken deep into the Earth through tectonic action. After many millions of years, volcanoes reprocess these rocks and return the CO_2 to the atmosphere as part of their gaseous outpourings.

When temperatures drop, as at the start of the Huronian glaciation, chemical weathering slows down because the chemistry involved is partly driven by temperature, but the volcanoes continue to release the previously stored CO_2. This builds a larger greenhouse effect, boosting the temperature and ending the ice age.

Such effects convince Kasting that the regulatory role of CO_2 holds the key to the faint young sun paradox. "Carbon dioxide will always tend to rise to a level that keeps the Earth from freezing," he says.

ÁRON SÜVEG/ANZENBERGER/EYEVINE

Home and dry

Water was probably the last thing the first life needed, says Colin Barras

"SOME warm little pond." Charles Darwin's speculative description of life's cradle, in a letter written to the botanist Joseph Hooker in 1871, still chimes today. Seed a watery environment with the right ingredients, Darwin mused, then cosset it with a little light, heat or electricity, and a purely chemical miracle of creation might occur.

Hard and fast evidence of how and where on Earth inanimate matter became animate is hard to come by. Other backdrops for life's first steps have gained in popularity since Darwin's time – around submarine hydrothermal vents, in ice or on Earth's radioactive first beaches,

Did life's cradle look like Death Valley?

for example. If pressed, though, most of us would still plump for the primordial soup.

In the intervening years, we have devised more detailed recipes showing how the early Earth might have cooked up simple organic molecules, and how these might have reacted further to form the more complex building blocks of life: things like amino acids, DNA and RNA. Besides the right chemical ingredients, the process needs warmth, sunlight, perhaps a little lightning and, most importantly, H_2O. Water is, after all, the essential solvent that underpins carbon-based life.

For Steven Benner, that is all a fairy tale. "We tend to think that water's properties are ideal for life, but the opposite is true," he says. "Water is corrosive." Benner is a chemist at the Foundation for Applied Molecular Evolution in Florida and for three decades he has been doing pioneering work in synthetic biology, which aims to recreate life's chemistry in the test tube. And he is no lone voice. As water's deleterious effects have become more apparent, many researchers are asking: is it time to dry out life's recipe?

Around 70 per cent of our planet's surface is ocean, and water makes up 60 per cent of our body weight. Few living things can survive for long without water: it is a perfect medium in which organic molecules can dissolve and react to sustain the core processes of life on Earth.

But this perfect solution is also a problem. Life's molecules don't just dissolve in water; the electron-rich oxygen of its molecules attacks them, and they begin to fall apart. "In your body right now, the DNA in your cells is losing an amino group many times a second because of the action of water," says Benner. Living things keep their molecules intact only through clever chemical strategies that perpetually repair the breakages.

Tricky when wet

The first life on Earth wouldn't have had time to develop those strategies. According to the widely accepted "RNA world" theory, RNA was the first self-replicating molecule, and a precursor to today's DNA-based life (see "Dawn of the living", page 10). Like DNA, RNA is built up from nucleotides, complex organic molecules that are themselves formed from two simpler components, a nucleobase and a sugar called ribose. Decades of research have shown that making nucleotides in water is a very tricky business. Individual steps can be made to work, but they don't all gel together. "We are still at the stage of scraping out the product of step seven, and carefully spooning it into the flask to begin step eight," says Benner. Fail to spoon in just the right amounts of various molecules at the right time, and the end result is a gunky mess.

In 2004, Benner made a breakthrough. He showed that borates – minerals containing varying proportions of boron and oxygen – could act as scaffolds for the construction of ribose, making that part of the chemistry a much more hands-off, naturally plausible process. The problem of attaching the ribose to the nucleobases remained, however, until in 2012 Benner made a simple and bold suggestion: to make life, just remove water. By replacing it with an organic solvent richer in carbon and poorer in oxygen such as formamide (CH_3NO), the right components would, in theory at least, stick together spontaneously to make RNA. This idea was bolstered by seminal work in 2015 showing that a simple set of chemical reactions can yield all the important building blocks of life, but only when the conditions are dry or nearly dry for some stages of the reaction.

Formamide would have been created when hydrogen cyanide in Earth's early atmosphere mixed with water. Its boiling point is higher than that of water, so in a hot environment the formamide would have become more ›

WORLDS WITHOUT WATER

Evidence that drinkable water once flowed on Mars, as found by NASA's Opportunity rover, is still lapped up as suggesting the planet could have harboured life. But with the realisation that water may have hindered early life on Earth (see main story), should we be looking elsewhere?

In fact, astrobiologists at NASA and elsewhere have long discarded the assumption that life needs aqueous chemistry. Earth and Mars aside, the solar system body thought most likely to harbour life is Titan, Saturn's largest moon. The Cassini probe, in orbit around Saturn since 2004, has shown Titan's dense atmosphere veils rough terrain but also smooth seas filled not with water, but the hydrocarbons methane and ethane. "Titan is an excellent place to explore for non-aqueous experiments in chemical self-assembly," says Jonathan Lunine, a planetary scientist at Cornell University in Ithaca, New York.

Lab experiments confirm that amino acids, the basis of proteins, could be generated on the surface of Titan, although temperatures are so frigid – as low as -180 °C – that life there would probably not be able to operate on Earth-like chemical principles. Covalent bonds of the sort that underpin our carbon chemistry would not form and break quickly enough, but weaker van der Waals bonds would be more stable and could play a more prominent part.

Whether life's origins were wet, dry or something else altogether, the different sorts of chemistry that might support life mean we should keep an open mind when considering the 2000-odd planets that missions such as NASA's Kepler space telescope have now found orbiting other stars, very few of which look like Earth. "We cannot limit ourselves to what we know in exploring the unknown," says Lunine. "We cannot simply search for the keys to life's origins underneath the narrow beam of the aqueous street lamp."

"The search for life beyond our planet has traditionally followed the mantra 'follow the water'"

concentrated as the water evaporated away. Borates are scattered across Earth's surface today, where they result mainly from the erosion of igneous rocks. Looking at Earth now, Benner has found one environment that combines both sweltering conditions and the presence of borates. It aptly sums up how unexpected life's earliest requirements might have been. Its cradle, says Benner, might have looked a lot like California's Death Valley.

Benner's chemistry arguably provides the first one-pot recipe for life that can bubble away without human intervention. Armen Mulkidjanian, a chemist at the University of Osnabrück in Germany, is a fan. But he points to a problem with cooking it up in a primeval Death Valley. "The world's borate minerals are all found in relatively young rocks," he says. There is no evidence that surface concentrations of borates were sufficient for the chemistry to work until about 3 billion years ago, he says – around a billion years after life supposedly got started.

So where then? Mulkidjanian sees inspiration in the geothermal fields of Kamchatka in eastern Russia. These are spots where fluids have flowed through Earth's crust and come to the surface as vapours, bringing with them nutrients accumulated from rocks along the way. Borates are often found in these geothermal fumes, as are the chemical components of formamide. One further chemical convergence emboldens Mulkidjanian in thinking that a similar environment could have cradled life: the geothermal fields of Kamchatka are just about the only place on Earth where the balance of sodium and potassium ions matches that inside living cells.

Mulkidjanian's twist on Benner's tale has gained supporters. "What's nice is that geothermal fields provide a constant set of conditions for the origin of life, since the chemistry is coming from Earth's stable interior and not its exterior," says Ernesto Di Mauro at the Sapienza University of Rome, Italy. "If you frame Benner's proposal in these geothermal fields, you have a scenario that doesn't have many weak points."

But not so fast. These scenarios require Earth to have supplied dry environments like a Death Valley or a Kamchatkan geothermal field 4 billion years ago. Until recently, the consensus would have been that this was no problem: Earth was then exiting an interval dubbed the Hadean because of its hot and hellish conditions. But in the past decade, geologists have cooled on the idea of a hot young Earth. Their main evidence comes from tiny crystals, each less than a millimetre across, of a mineral called zircon. These are tough, easily outlasting the rocks they formed in, which have been obliterated by subsequent tectonic activity.

A close look indicates that the crystals were made in cool, soggy conditions, implying that Earth's early history was wet, with land accounting for perhaps just 5 or 10 per cent of its surface. Joseph Kirschvink, a planetary scientist at the California Institute of Technology in Pasadena, goes so far as to speculate there was no dry land at all. That leads him to a seemingly way-out conclusion: if the first life needed to be dry, it cannot possibly have started on Earth.

Premature requiem

The search for life beyond our planet has also traditionally followed the mantra "follow the water" – although recent discoveries in and out of the solar system are causing that assumption to be revisited (see "Worlds without water", above). Kirschvink has been an enthusiastic supporter of the idea that Earth's life possibly began on Mars, ever since the infamous announcement in 1996 that fossilised "microbes" had been discovered in a 4.1-billion-year-old Martian meteorite called ALH 84001. The consensus now is that these are just rock features that look like cells – but we should not discount the Martian option just on that basis, according to

"If life needed a dry place to get started, Mars had the right conditions at the right time"

Kirschvink. "The requiem for life on Mars was very premature," he says.

And if life needed a dry place to get started, Mars had the right conditions at the right time. Although it once had an ocean basin around its north pole, its southern highlands were almost definitely never submerged. "The RNA world would have done very well there," says Kirschvink. He thinks that later on, probably after the RNA world had given rise to the DNA-based cellular life we are familiar with today, an asteroid hit the Martian surface, throwing chunks of rock and ice containing these cells beyond the planet's atmosphere. Perhaps as little as nine months later, some of them made it to Earth.

In 2013, at the Goldschmidt geochemistry conference in Florence, Italy, Benner agreed that there is logic to Kirschvink's arguments. "The evidence seems to be building that we are actually all Martians; that life started on Mars and came to Earth on a rock," he said, generating a wave of media interest.

Just weeks before the conference, James Stephenson, now at the NASA Ames Research Center, California, and his colleagues had provided further succour for the theory, with confirmation that Mars is rich in a key ingredient for Benner's pathway. They published an analysis of a 1.3 billion-year-old Martian meteorite called MIL 090030 that showed it was riddled with boron. "I was honestly surprised that people hadn't really looked at boron in Mars samples before," says Stephenson. He hopes to collaborate with Benner soon to develop the idea further.

Mulkidjanian agrees that conditions on early Mars may have been suitable for the origin of life, and wryly points to evidence that the planet may even have had geothermal fields similar to those in Kamchatka, his favoured sort of cradle for life.

But he questions whether dry life arriving on a wet Earth on a Martian meteorite could have assimilated well. Genomic studies show that life on our planet traces back to a collection of cells that survived by sharing the products of their genes, creating a single-celled organism referred to as the last universal common ancestor (See "Meet your maker", page 6). "If you dropped a primitive Martian cell into Earth's oceans, it is highly unlikely that it would have proliferated alone," he says. Rather, it would take a whole microbial ecosystem arriving, intact, from Mars.

MICHAEL MELFORD/NATIONAL GEOGRAPHIC CREATIVE

Geothermal chemistry might have fitted the first life perfectly

Back to Darwin

This hints at a wider problem. No matter where and on what planet the delicate early forms of life originated, water's corrosive nature would have caused them to struggle when first introduced to a wet environment. All indications are that this happened very early: life has thrived in the oceans for billions of years. "There is a paradox," admits Benner. "You have to get out of water to solve the water problem, but then you've got to get back into the water." The only real solution, he says, is to gradually moisten a dry cradle and allow the variety of molecules to either cope or perish through natural selection.

Or we tweak our story still further. Nicholas Hud, a chemist at the Georgia Institute of Technology in Atlanta, points out that most researchers accept that DNA somehow evolved from RNA, so we should at least consider the possibility that RNA evolved from a different molecule that was stable in water. "When I look at RNA, I see a molecule that is perfect at what it does, but that's hard to make," he says – perhaps a telltale sign that natural selection helped shape RNA. "Which is more probable? Life began on Mars, was transported to Earth and picked up where it left off, or life began on Earth, but with a molecule different from RNA?"

Hud's thinking could remove the need for Kirschvink's Martian scenarios and Benner's chemistry, but would demand a rethink of the underlying assumption that life's chemical origin lies with RNA. It would seem fitting, though, that the ultimate solution to the water problem, even before life as we know it got started, could lie in the principles of natural selection. Stories about the origins of life begin and end with Darwin. ■

CHAPTER TWO

THE HISTORY OF LIFE

THE planet is in crisis. The stench of death is everywhere as whole branches of the tree of life are pruned almost to oblivion – and all because of the waste gas pumped into the atmosphere by one incredibly successful species. Welcome to Earth, 2.4 billion years ago.

This was arguably the most tumultuous episode in life's history. It had been thriving for well over a billion years when a new kind of cell appeared on the scene, one that harvested the sun's energy using a process that generates a highly toxic by-product – oxygen. These cells were soon growing in such unimaginable numbers in the primordial oceans that they transformed Earth's atmosphere.

At the time, this was a catastrophe. The rise of oxygen may have wiped out a greater proportion of life than in any other mass extinction. But the very property that makes oxygen so dangerous – its high reactivity – also makes it a rich source of energy. Life soon started to exploit this, including, of course, our animal ancestors.

In the past 15 years, our view of this crucial episode has been turned upside down. The textbooks will tell you that oxygen levels began climbing soon after photosynthesis evolved, but we now know that some cells started photosynthesising as long as 3.4 billion years ago, long before oxygen levels began to rise. The question is, why did it take so long for them to start pumping out oxygen?

At its heart, photosynthesis is about harvesting the sun's energy. Plants use this energy to make food, by building chains of carbon from carbon dioxide. The process produces sugars that can be used as an energy source or to make more complex molecules, from proteins to DNA. But contrary to what you might expect, it does not necessarily produce oxygen. In fact many bacteria turn light and CO_2 into food without producing oxygen. What's more, recent discoveries suggest they have been doing so for nearly as long as there has been life on Earth.

In 2004, Michael Tice and Donald Lowe, both then at Stanford University in California, were studying rocks in South Africa that formed in shallow water 3.41 billion years ago. They found fossil structures rather like the microbial mats formed by photosynthetic bacteria today, but no sign that any oxygen was produced. The most likely explanation, they think, is that these cells were carrying out anoxygenic photosynthesis.

Since that discovery we have actually come face-to-face with some of these early photosynthetic microbes. In 2011, Martin Brasier at the University of Oxford and colleagues discovered fossils of individual

Rise of the water eaters

Ripping water apart to release oxygen is incredibly hard, but we wouldn't be here if life hadn't learned to do it. Colin Barras has the scoop

MICHAEL MELFORD/NATIONAL GEOGRAPHIC STOCK

These photosynthetic bacteria produce sulphur, not oxygen

bacterial cells in rocks that formed 3.43 billion years ago, in what is now western Australia. "They occurred in a well-lit intertidal or supratidal setting," Brasier said at the time. The chemical make-up of the rocks, along with the plentiful light, strongly suggests that some of the cells photosynthesised without producing oxygen.

It may seem surprising that anoxygenic photosynthesis evolved so soon after life itself – the earliest fossils we know of are only slightly more ancient, at 3.49 billion years old. But Nick Lane of University College London, who studies life's origins, thinks that once cells capable of living on chemical energy had evolved, it was not a huge step for them to start exploiting light energy instead. "Really, light just gets electrons flowing through the same equipment," he says.

For researchers like Lane, the mystery is instead why it took so long for the oxygen-producing form of photosynthesis to evolve. It may not have emerged until around 2.4 billion years ago, perhaps a billion years after anoxygenic photosynthesis appeared. Given the advantages of oxygen-producing photosynthesis, why the delay?

Photosynthesis has two main steps. In the second, electrons are added to CO_2 to help convert the molecule into sugars. The first step is getting the electrons. They are stripped from a source molecule and used to generate an electrochemical gradient that powers the second step.

The billion-year delay

In oxygenic photosynthesis, the source molecule is water. Removing electrons splits water molecules into hydrogen ions and oxygen gas. The hydrogen ions and electrons play a key role in turning CO_2 into sugars. The oxygen, though, is an unneeded by-product.

In anoxygenic photosynthesis, different molecules provide the electrons. One of the most common donors is hydrogen sulphide. Splitting it generates sulphur as a waste product instead of oxygen. The advantage of hydrogen sulphide is that it is very easy to remove electrons from, or oxidise. It was also common in the early ocean, but probably got used up quickly in surface waters where anoxygenic photosynthesis took place.

The great advantage of using water as the electron donor instead is that there is an

endless supply of it in the oceans. But there is a big drawback, too. "Water is incredibly difficult to oxidise," says Robert Blankenship at Washington University in St Louis, Missouri. We're still struggling to do it: researchers have been trying for decades to develop cheap, energy-efficient ways of splitting water to produce hydrogen gas for fuel.

So it makes sense that photosynthesising bacteria first exploited easy-to-oxidise molecules before switching to water. The conventional view, supported by Blankenship and many other researchers, is that oxygenic photosynthesis gradually evolved from the anoxygenic version through a series of intermediate steps. But while at Queen Mary, University of London, John Allen devised an alternative scenario that is almost deliberately implausible. "This process has to have happened by accident," he says – only that can explain the billion-year delay.

Any scenario for how oxygenic photosynthesis got started has to deal with four significant facts. Fact one: there are two related but distinct types of anoxygenic photosynthesis. Some bacteria have what is called a type-I reaction centre, which takes electrons from sources like hydrogen sulphide and sends them down a one-way street: each electron is used just once. Other bacteria carry a type-II reaction centre that recycles electrons internally, making them less dependent on an external electron source (see illustration, above right).

Fact two: oxygenic photosynthesis involves a type-I and a type-II reaction centre working in tandem. Fact three: even though cyanobacteria have both reaction centres, it is only the type-II centre that splits water and generates oxygen, at a site that contains four manganese atoms arranged around a calcium atom. Finally, fact four: anoxygenic photosynthetic bacteria that have a type-II reaction centre lack this cluster of manganese and calcium.

Blankenship thinks it is the final two facts that are most important and point towards a simple scenario. The type-I centre evolved first, he thinks. Then the genes encoding its machinery were acquired by another group of bacteria – gene-swapping was and is rife among bacteria. In this group, the machinery gradually became modified, forming the first type-II reaction centre. Later, the descendants of these bacteria began to incorporate metal atoms into it. Eventually they arrived at a configuration that included four atoms of manganese and one of calcium. They could now oxidise water and perform oxygen-generating photosynthesis using just a type-II reaction centre.

Only later, claims Blankenship, did this group's descendants acquire the type-I machinery via gene transfer, giving rise to cyanobacteria. So Blankenship thinks it is just a coincidence that cyanobacteria have two different reaction centres.

"Bacteria have been photosynthesising for nearly as long as there has been life on Earth. So why did it take a billion years for them start making oxygen?"

This scenario makes one clear prediction – there were once bacteria that generated oxygen through photosynthesis, but were distinct from cyanobacteria. They would have been the missing link between the anoxygenic bacteria with a type-II reaction centre – including what are called purple bacteria, alive today – and the oxygen-generating cyanobacteria, so let's call them "indigo" bacteria. No indigo bacteria have ever been found, though. Instead, Blankenship and others have tried to show that they could have existed.

Perhaps most significantly, a team at Arizona State University in Tempe has tried to turn a purple bacterium into something like an indigo bacterium. The researchers modified the purple one so it could bind a manganese ion to its reaction centre and use it to react with molecules containing oxygen. It's not oxygenic photosynthesis, but it's a step towards it.

Marine disaster

Even if biologists do one day engineer an indigo bacterium in the lab, though, this wouldn't prove they could evolve naturally. And to Allen, the gradual evolution scenario cannot explain all the facts. Why would such an apparently simple sequence of events have taken up to a billion years to occur? Why did oxygenic photosynthesis evolve only once, in cyanobacteria, as far as we know? (Plants acquired the ability to photosynthese by allowing cyanobacteria to live inside them – their chloroplasts are descended from cyanobacteria.) And why do all cyanobacteria have both kinds of reaction centres?

Allen also thinks the type-I centre evolved first. But from there, his scenario is very different. Allen thinks that early in their history, these bacteria experienced some kind of genetic glitch which duplicated the entire set of genes for making a type-I reaction centre. The spare copy was free to take on a different role, and it evolved the ability to recycle electrons – the first type II reaction centre. Having two distinct reaction centres allowed these "proto-cyanobacteria" to thrive in a wide range of environments, Allen proposes. When there was plenty of hydrogen sulphide, they used their type-I reaction centre. When hydrogen sulphide ran low, the bacteria switched to using their type-II reaction centre.

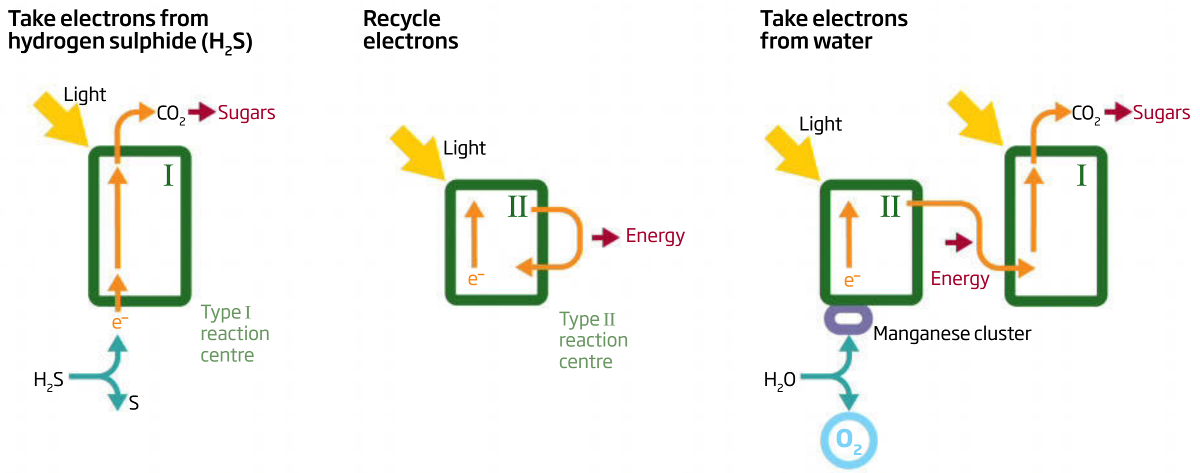
Then one day, disaster struck: some proto-cyanobacteria drifted into a shallow marine environment rich in manganese but poor in hydrogen sulphide. The bacteria duly switched to a type-II reaction. But when ultraviolet light hits manganese it strips off electrons, so there were actually plenty available – and these electrons quickly clogged the cyclic type-II reaction centre. The resulting manganese ions would have reacted with water to form manganese oxide, but there was plenty more manganese around, producing enough electrons to kill the microbes.

Well, almost all of them. One lucky proto-cyanobacterium survived, Allen suggests, because a mutation wrecked the switch that turned on only one kind of reaction centre at

Plants can harvest light only with the help of symbiotic

Three ways to harvest light

There are several forms of photosynthesis, but only one makes oxygen as a by-product



Done by	Green sulphur bacteria	Purple bacteria	Plants, algae, cyanobacteria
Advantage	H_2S is easy to split	No electron source required	Unlimited supply of water
Disadvantage	Supply of H_2S is limited	Provides energy only. Other reactions needed to turn CO_2 into food	Water is hard to split

any time. With both kinds in action together, electrons from the manganese could flow through the type-II centre before being siphoned off by the type-I centre, preventing a blockage. In other words, the two reaction centres would have been working together, just as they do in cyanobacteria today.

But how did the descendants of this bacterium go from getting electrons from manganese to getting them from water? Well, in a way they didn't. To this day manganese provides the electrons needed for photosynthesis in all plants. However,

FRANK KRAHMER/GETTY

the electrons now come from a cluster of manganese atoms within the type-II reaction centre, and this cluster has a remarkable ability – after it has given up electrons, it steals others from water molecules, splitting them apart and liberating oxygen.

Once early cyanobacteria had evolved this kind of type-II centre, they needed only trace amounts of manganese. They could then spread from manganese-rich environments and start exploiting the abundant CO_2 available at the time, with the help of an unlimited supply of water and sunshine. Soon immense numbers of cyanobacteria were spewing out enough oxygen to transform the atmosphere.

If Allen's hypothesis is correct, proto-cyanobacteria had to stumble into a highly unusual manganese-rich environment and lose control of a key genetic switch at the same time. Allen agrees this is improbable, but this could be why oxygenic photosynthesis took a billion years to appear. "The way I look at it, it was only a matter of time until one of these bacteria had two accidents at once," he says.

Remarkably, there is now hard evidence to back Allen's idea: we've found one of those rare manganese-rich environments. Woodward Fischer at the California Institute of Technology in Pasadena and his colleagues have been studying rocks laid down in what is now South Africa just before levels of oxygen began to rise. In one spot they found a superabundance of manganese oxide in rocks that formed, significantly, in the absence of oxygen. Not even ultraviolet light could have generated manganese oxide on the scale found in the rocks. This leaves photosynthesis as it existed in Allen's proto-cyanobacteria as the only plausible scenario, the team told a meeting in December 2012.

"It is big news, hugely exciting – and spot on for John's hypothesis," says William Martin at the University of Düsseldorf, Germany, who studies early evolution. But Blankenship is sticking to his guns. He describes his many discussions with Allen and Martin on the origin of oxygenic photosynthesis as "very spirited, yet friendly".

What would settle the debate once and for all is the discovery of living representatives of one of the proposed intermediate forms – either indigo bacteria or proto-cyanobacteria. Surprisingly, Blankenship and Allen are both confident that their respective organisms still exist somewhere in the world. "You find specialist environments today that correspond to typical conditions 2.4 billion years ago," says Allen. "It's not absurd to think that these microorganisms are still out there."

A boost for this idea came in 2013 with the discovery of a new group of bacteria that are the closest relatives of cyanobacteria. Interestingly, these melainabacteria don't seem to have genes for photosynthesis. "This suggests that cyanobacteria developed their photosynthetic capability via horizontal gene transfer from other organisms, after they split from melainabacteria," says Blankenship.

Whatever the ancestor of cyanobacteria turns out to be like, we have reason to be very grateful to it. "This organism – maybe by accident – was hugely important," says Allen. "Quite simply, it changed the world forever." ■

Oxygen is supposed to have driven the evolution of complex life. Great story, says biochemist Nick Lane, but it's wrong

Genesis revisited

BRIAN LAROSSA

GO WEST, young man! More specifically, go about 200 kilometres west of Crete, then straight down to the bottom of the Mediterranean Sea 3.5 kilometres below. There you will find a lake with some extraordinary inhabitants.

Around 6 million years ago when the Mediterranean nearly dried up, vast amounts of salt were deposited on the sea floor. Some of these deposits were exposed about 30,000 years ago. As this salt dissolves, extra-salty, dense water is sinking to the depths, forming a brine lake 100 metres deep. Even more surprising than the existence of this lake beneath the sea, however, is what lives in it.

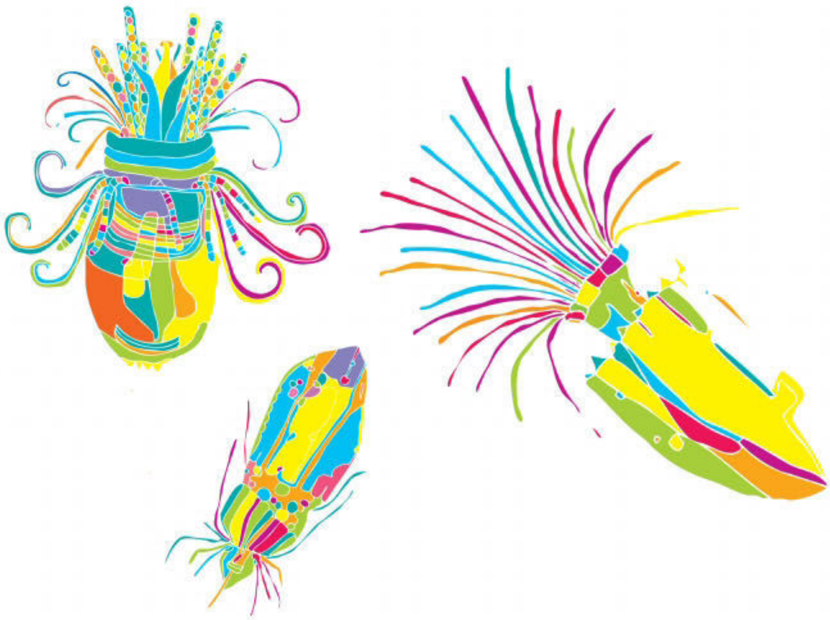
The water in the brine lake does not mix with the water above and so ran out of oxygen long ago. Instead, the toxic gas hydrogen sulphide oozes from the black mud. It's the last place you would expect to find animals. But that's exactly what has been discovered: the first animals, as far as we know, that can grow and reproduce without a whiff of oxygen.

These tiny mud-dwellers are far more than a curiosity. They could be the best pointer yet to the origin of complex cells: the basis of most life on Earth, from amoebae to oak trees.

"The ecology is interesting, but the real significance of these critters is what they say about evolution," says Bill Martin, an evolutionary biologist at the University of Düsseldorf in Germany. For Martin, the discovery is a beautiful affirmation of a radical prediction he made more than a decade ago – that oxygen had nothing to do with the evolution of complex life.

The first kinds of life on Earth, the bacteria and archaea, were simple cells – not much more than bags of chemicals. Eventually, they gave rise to complex cells, or eukaryotes, with sophisticated internal structures, the kind of cells found inside all plants and animals. And one of the most important events in the evolution of complex cells was the formation of a symbiotic union between a host cell and a bacterium – the ancestor of the cellular powerhouses known as mitochondria, which extract energy from food using oxygen.

"Burning" food provides 10 times as much energy as alternative ways of extracting energy from food without oxygen. When complex cells gained this ability, it changed the course of life on Earth: without mitochondria, large active animals might never have evolved (see "Living without breathing", page 35). It is not surprising, then, that most biologists think that the original symbiotic union



"Clearly, the existence of animals that don't need oxygen means oxygen is not the be-all and end-all of complex life in the universe"

some single-celled organisms have structures that resemble mitochondria but do something quite different; they generate energy without using oxygen, by breaking food down into carbon dioxide and hydrogen – so Müller called them hydrogenosomes.

Before hooking up with Martin, Müller had gone on to show that hydrogenosomes do not merely resemble mitochondria but are in fact stripped-down mitochondria. They have the same shell, yet completely lack the usual ATP-generating machinery driven by oxygen. Instead, they have machinery that generates ATP while creating hydrogen as waste. The question is, was this different machinery acquired as mitochondria evolved into hydrogenosomes, or was it present all along? And if it was present all along, then what did the bacterial ancestor of the mitochondria actually look like?

Martin and Müller leapt straight in at the deep end. The ancestor of mitochondria, they said, was a versatile bacterium capable of living in a variety of environments – it could use many substances, including oxygen, to produce energy, and it could make hydrogen too. This is hardly an imaginary superbug: existing bacteria like *Rhodobacter* can do all that and more.

The ability of ancestral mitochondria to make hydrogen, rather than use oxygen, was the basis of the primordial pact that gave rise to the eukaryotes, Martin and Müller argued. The bacteria produced hydrogen as waste, and the host cell used it to convert carbon dioxide into methane, gleaning a little energy from the process – just as many archaea, called methanogens, still do. The symbiosis began in an environment with little or no oxygen and only later, after the relationship was well established, did the host cell start exploiting the ability of the ancestral mitochondria to use oxygen.

This idea, known as the "hydrogen hypothesis", was proposed by Martin and Müller in 1998, but it has never gained widespread acceptance. It was not just up against the gut feeling of most researchers that the rise of the eukaryotes was related in some way to oxygen; on the face of it, what little evidence there was did not support it either.

Most studies of the genes needed to make hydrogenosomes, for example, suggest they evolved repeatedly and independently from mitochondrial genes, with some extra ones being picked up by lateral gene transfer from other organisms along the way. "I think the transformation from aerobic mitochondria to hydrogenosomes has little or nothing to do with the origins of eukaryotes," says microbiologist Mitch Sogin at the Marine Biological Laboratory in Woods Hole, Massachusetts.

Not surprisingly, Martin disagrees. "Single gene studies are subject to so many artefacts

revolved around oxygen. According to Martin, though, they are utterly wrong.

The narrative in the textbooks seems compelling. In the beginning, so the story goes, there was no oxygen. The evolution of photosynthesis changed all that. By releasing their waste – oxygen – into the air, cyanobacteria transformed the globe around 2.3 billion years ago. As oxygen levels rose, the toxic gas caused the first mass extinction, wiping out nearly all existing organisms and paving the way for a new lifestyle: extracting energy from food using oxygen.

The bacteria that evolved this ability were preyed on by other cells. At some point, one cell failed to digest its dinner and instead let the bacteria live on inside it. This host cell, so the story goes, got two huge benefits: protection against oxygen, which was guzzled up by the ancestral mitochondria, and a share of the extra energy its guests could extract from food using oxygen.

It was not until oxygen levels rose even higher, around half a billion years ago, that the oceans could support large multicellular organisms that got their energy by burning food. That led to the Cambrian explosion, when all kinds of animals appeared. The main point about this story is that it sweeps forward with a magisterial inevitability, waiting only on a rising tide of oxygen.

The broad outlines are true. Oxygen levels did rise in two steps; most eukaryotes do generate energy using oxygen, and are normally tolerant of its toxicity; and the earliest fossil animals did appear soon after a big rise in oxygen levels in the oceans. Yet there are grounds to suspect that oxygen was not the puppet master after all.

One is that the initial rise in oxygen did not cleanse the oceans, but converted them into a stinking mess, full of hydrogen sulphide. Far from having few refuges, anaerobes had whole oceans to themselves. What's more, these conditions lasted for more than a billion years, right through the period when the eukaryotes are thought to have evolved.

No free lunch

Another issue is that oxygen is not particularly toxic by itself – it needs to be converted into free radicals before it will react with and destroy proteins and DNA. Mitochondria generate lots of free radicals so, far from protecting their hosts from oxygen, their ancestors would have increased the damage it does. In any case, consuming oxygen merely steepens the diffusion gradient; it's like trying to save yourself from drowning by drinking the surrounding ocean.

Even the power advantage of oxygen is problematic. No bacterium gives away energy for free, so the host cell could not have benefited from oxygen respiration until it had evolved the kit needed to siphon off energy-rich ATP from its guest bacteria. In the meantime, the "symbiosis" would have been a disaster. Thanks to their ability to exploit oxygen, the bacteria would be likely to outgrow the host and end up killing it.

So if the union was not about oxygen, what was it about? Hydrogen, according to Martin and Miklos Müller of The Rockefeller University in New York.

Back in the 1970s, Müller discovered that

that we can conclude almost nothing about deep evolutionary history from them," he says. "Line up the same genes from the other end and you derive a totally different tree."

What's more, if aerobic mitochondria have evolved into hydrogenosomes on many separate occasions by picking up genes from other organisms, then why do hydrogenosomes always have the same small subset of genes for making hydrogen? They could have picked up all kinds of genes from bacteria, which have an amazing repertoire of metabolic abilities, Martin says, so why pick the same ones each time?

Remarkable abilities

Martin's explanation is simple: they share the same set because they inherited them from a single bacterium – the ancestor of mitochondria. For all its power, this argument is sterile without more evidence one way or another: you either believe it or you don't.

That evidence is starting to emerge. Take *Naegleria gruberi*, a curious shape-changing cell. In 2010 it was discovered that in the absence of oxygen, its mitochondria appear capable of generating energy by producing hydrogen, with the help of proteins also found in hydrogenosomes.

In the past few years, there have also been reports of the kind of large scale influx of genes that the hydrogen hypothesis predicts. In 2012, Shijulal Nelson-Sathi at the University of Düsseldorf, together with Martin and others, showed that the archaeon Haloarchaea had been transformed from strictly anaerobic to oxygen-using via the influx of a thousand bacterial genes. "This argues in favour of mass transfer of genes for entire pathways," says Martin. Likewise, 2015 research by Martin and others showed that the prokaryotic genes found in eukaryotes to enable photosynthesis and mitochondrial metabolism likely came about through episodic large scale transfer of genes, rather than gradual accumulation.

And now we have found animals that can live without oxygen lurking in brine lakes at the bottom of the Mediterranean. These species were discovered by marine biologist Roberto Danovaro of the Polytechnic University of Marche in Ancona, Italy, and his colleagues. They belong to an obscure group of microscopic animals, the Loricifera, found in ocean sediments around the world.

Little more than a millimetre long, the new species are so inactive that it took a while to prove they were indeed living, if not breathing. What's really striking about them, though, is not just their ability to live without oxygen but the way they manage it: unlike all other animals, including other loriciferans, they appear to have hydrogenosomes rather than mitochondria.

These recent discoveries are starting to transform people's perspectives. "The simplest explanation is that all the different types of mitochondria inherited their metabolic toolkits from a single versatile ancestor," says Mark van der Giezen at the University of Exeter, UK, who studies the evolution of anaerobic eukaryotes.

And if that is the case, then eukaryotes would have been able to live in anoxic environments right from the start. "Nobody seriously thinks that bacteria dwelling in such habitats only recently adapted to anaerobic niches," points out Martin. "But when it comes to eukaryotes, there is still a curious tendency to assume that they only invaded anaerobic niches of late. There's no logic in that."

Indeed, if the hydrogen hypothesis is right, the implications for complex life are striking. The existence of animals that don't need oxygen means that oxygen is not the be-all and end-all of complex life in the universe. The anoxic oceans a billion years ago might have been full of tiny creatures – as indeed many anoxic basins probably are today, if we look properly – and these animals got larger and more active when oxygen levels rose.

The deeper point relates to the origin of eukaryotes. There was no magisterial progression from simple to complex life as oxygen levels rose; no inevitability about it. Instead, there was a symbiotic union between a bacterium that could make hydrogen and an archaeal host cell that could exploit that hydrogen: a freak event that changed the world. ■

LIVING WITHOUT BREATHING

Some fish, mussels and sediment-dwelling worms can live without oxygen for hours or even days. Instead of getting energy by "burning" food, the cells of these animals switch to ways of producing energy that do not require oxygen. Until recently, no animals had been discovered that go their entire lives without oxygen (see main story) – it was thought to be impossible.

Oxygen is not only used for getting energy from food, it is also needed to make compounds like collagen, the "glue" that holds animals together. No oxygen, no collagen; no collagen, no animals, the thinking went. That must be wrong, although we have yet to work out how the newly discovered animals make compounds like collagen without oxygen.

So could there be planets out there with large animals that do not need oxygen? While burning food produces 10 times as much energy as other means like fermentation, in theory an animal might get around that if it could somehow get 10 times as much fuel. The trouble is, fermentation leaves far less energy for predators in ecosystems. With aerobic respiration, there can be five or six links in a food chain before the amount of energy falls below 1 per cent of that available initially. Without oxygen, this happens with just two links.

And with far less scope for predation, animals might not evolve as far or as fast; the need to find prey or dodge predators is thought to have driven the development of features like eyes and mouths and muscles.

ROBERTO DANOVARO

This little loriciferan can manage fine without oxygen

Life's long fuse

After 3 billion years, life evolved into giant, fractal creatures. What happened, asks James O'Donoghue

A FERN-LIKE impression appears in the rock face. Grasping at their rope, the boys very nearly miss it. It is April 1957 and three schoolboys are climbing in a quarry in Charnwood Forest in the English east midlands. Incredible as it would have seemed at the time, this serendipitous find was about to change our understanding of the history of life.

"Our reaction was, it's a leaf," says Roger Mason, who was 16 when he discovered the fossil and is now a professor at the China University of Geosciences in Wuhan. "We were surprised, but I didn't know enough about geology to realise how startling a discovery it was." A few days later he persuaded Trevor Ford of the nearby University of Leicester to have a look. Ford was sceptical. The Charnwood rocks were Precambrian, too old for fossils. Everyone knew that. But Ford was astonished at what he saw. The find was clearly a fossil resembling a fern frond about 20 centimetres long (pictured, page 40).

To understand the significance of finding a fossil like this in Precambrian rocks, you have to go back to the time of Charles Darwin. He was familiar with the mystery of the "Cambrian explosion" – the abrupt appearance in the fossil record of multicellular animals 542 million years ago. How could such diversity be seen in the Cambrian but not before? In 1859, Darwin wrote in *On the Origin of Species* that the Precambrian must have "swarmed with living creatures" that had not been preserved. The problem became known as Darwin's dilemma and remained a puzzle for nearly a century.

The boys' discovery set off a chain of research around the world, says Ford, who named the fossil *Charnia masoni*. "People started to look at Precambrian rocks again." Australian palaeontologists soon realised that they had already found similar fossils but had misdated them as Cambrian. These finds, from the 1940s, came to be known as Ediacarans, after their location in the Ediacara Hills of South Australia. The name stuck, and as scientists re-examined similarly aged rocks, they realised that Ediacarans could be found worldwide.

After 60 years of study, we now know a lot about the Ediacarans. They were, as far as we know, the first group of large-bodied life forms on Earth, appearing 580 million years ago and almost all had disappeared 39 million years later. Most were large and immobile. The largest were over 4 metres long, although most types would have fitted comfortably into a shoebox.

For everything we know about the Ediacarans, however, there are still many mysteries. For 3 billion years, life on Earth had been microbial. What caused the sudden increase in size and complexity? What kind ›

MARC BURKHARDT

MARC BURKHARDT

of creatures were the Ediacarans, and what led to their demise? Perhaps the biggest mystery of all is their biological affinity. Where do the Ediacarans fit on the tree of life, and how – if at all – were they related to the creatures of the Cambrian explosion?

Palaeontologists are now edging towards consensus on all these points. Most split the Ediacarans into two distinct groups with different evolutionary origins and histories. The first half of their reign was dominated by a type of deep-sea organism utterly different from any life form on Earth today. From about 555 million years ago, however, new shallow-sea types evolved, and some of them went on to inherit the Earth.

When the Ediacarans were first described, palaeontologists thought they could slot them comfortably into known animal groups. They were interpreted as primitive ancestors of the creatures of the Cambrian explosion: worms, corals, arthropods, jellyfish and the like. However, as more fossils were found, more and more peculiarities came to light, and doubts mounted. It became clear that the majority of Ediacarans were oddballs of uncertain affinity. In the mid-1980s, Adolf Seilacher of the University of Tübingen in Germany tore up the rulebook. He argued that even though Ediacarans resembled known animals, they were, in fact, a hitherto unrecognised and extinct kingdom of life – a dead-end experiment in evolution that disappeared at the end of the Precambrian.

Earliest Ediacarans

For much of the past 30 years the debate has been polarised between those who believe that Seilacher was correct and those who maintain that the Ediacarans are the "long fuse" of the Cambrian explosion. It turns out that both camps are, to some extent, right.

The breakthrough began in 2003 when Guy Narbonne of Queen's University in Kingston, Ontario, Canada, and Jim Gehling of the South Australian Museum in Adelaide reported the discovery of the oldest known Ediacaran fossils. They had been scouring Mistaken Point on the Avalon Peninsula in Newfoundland, Canada, a spot already well known for Ediacaran fossils, when they found a cache of fossils that date back around 580 million years, more than 10 million years older than the previous oldest.

You might be forgiven for expecting the earliest complex life on Earth to be quite small. Narbonne and Gehling certainly did, but they were wrong. "Our search image was for things about the size and shape of our thumbnails," says Narbonne. "Instead, we came up with 2-metre-long fronds."

Those giant fronds looked similar to *Charnia masoni*, the original Ediacaran, but were about 10 times longer. They also discovered a solitary specimen of a 4-metre-long fossil that looked a bit like a champagne flute. It is the biggest Ediacaran ever found, but beyond that its identity is a mystery.

The two giants weren't the only new species. There was *Thectardis*, which is the size and shape of an ice cream cone, and a disc-like organism, *Ivesheadia*, which has the size and appearance of a pizza, complete with a circular crust and pepperoni.

Younger rocks at Mistaken Point also contain similar, though more diverse, creatures: a host of other discs and fronds, the cabbage-shaped *Bradgatia* and several new creatures, including one like a spindle and another like a feather duster. Together, these first Ediacarans are known as the Avalon assemblage and are the earliest undisputed, large, complex life forms on Earth.

So what were the Avalon life forms like? Analysis of the sedimentary rocks showed that they dominated the deep waters until around 560 years ago, living an estimated 500 metres to 2 kilometres down. They did not move, either lying on the seabed or hovering above it, anchored by a holdfast. The fronds resemble ferns or seaweed but they cannot have been either: water at that depth would have been too dark for photosynthesis.

In 2003, a team led by Narbonne studied more than 100 fossil beds at Mistaken Point to try to work out how the early Ediacarans made a living. They found that although these Ediacarans may not have looked like animals, they certainly acted like them. They were either bottom feeders or fed on organic matter in the water column, just as in modern marine environments. "Ecologically they behave more like animals than anything else," says Narbonne.

In other respects, however, they are distinctly unlike animals. Kevin Peterson of Dartmouth College in Hanover, New Hampshire, has found that the Avalon creatures did not have any animal-like means of capturing or eating food: no appendages for grabbing, no mouth, no gut and no anus. Nor did there appear to be anything controlling their growth. Nearly all animals stop growing when they reach a certain size: not so with these organisms. In these important respects, they resemble fungi rather than animals. Scientists had to conclude that they could not place them with any living types of animal.

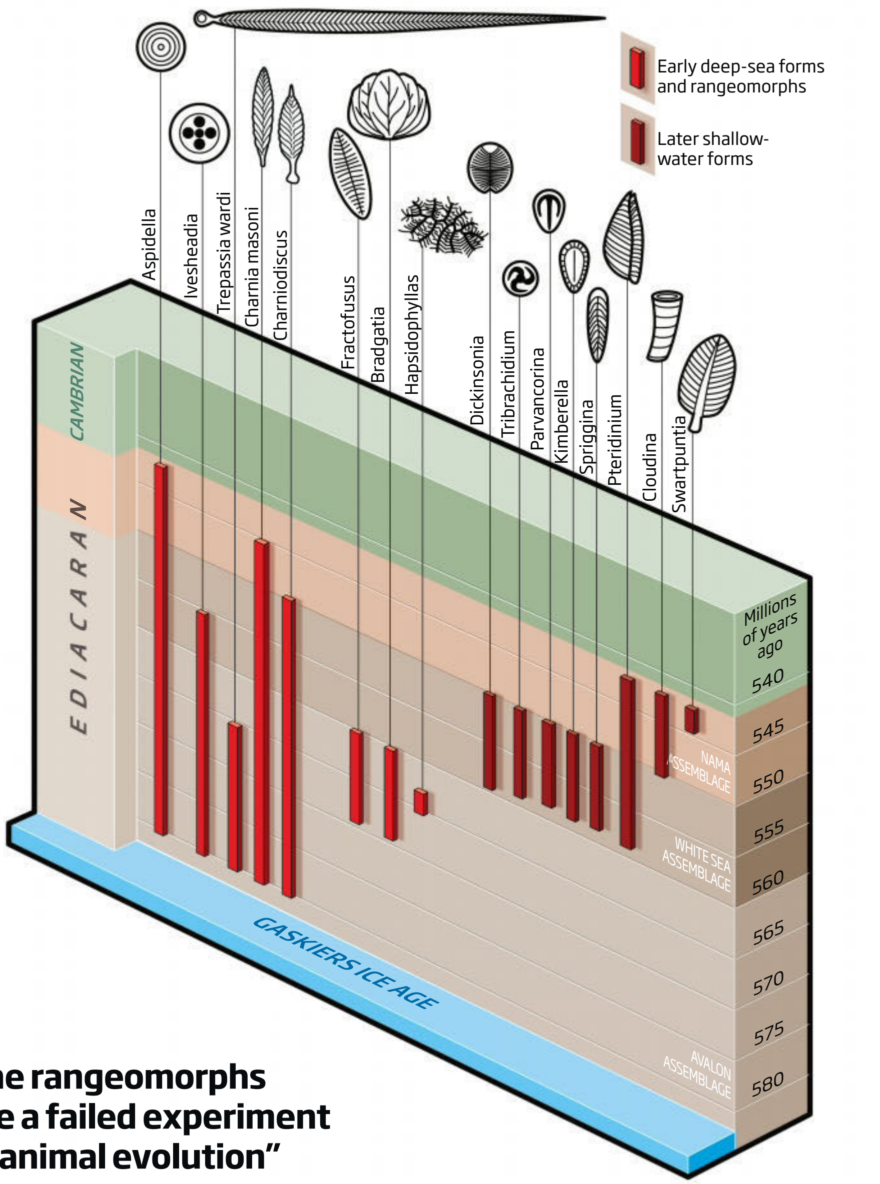
Then, in 2004, came a spectacular discovery. At another Newfoundland location called Spaniard's Bay, Narbonne found a group of around 100 frond-shaped fossils in an exquisite state of preservation. Ediacaran fossils are nearly always buried in coarse-grained sediment that does not show very much detail, but the new fossils were different. Details as fine as one-thirtieth of a millimetre were preserved, meaning that Narbonne could work out how these organisms were built.

He found that they were made in a completely different way from other animals: they were fractal. Each frond was built up from smaller, identical fronds, and each of these was composed of yet smaller fronds, and so on, down to the smallest scale visible. Narbonne called these fossils "rangeomorphs" after a similarly frondy fossil called *Rangea* that had been described years earlier.

There was more. When Narbonne re-examined the Mistaken Point fossils, he found that almost all the species shared the same fractal construction. "It's like something out of science fiction," says Narbonne. "Imagine inventing a completely different way of making animals. Yet this really did happen and it dominated life for 20 million years."

Parallel worlds

The mysterious Ediacaran fauna is made up of two distinct groups. One evolved in the deep sea 580 million years ago and left no ancestors. The other appeared in the shallows 20 million years later and lit the fuse of the Cambrian explosion



"The rangeomorphs are a failed experiment in animal evolution"

Many researchers are coming round to the view that the rangeomorphs were a unique group unlike anything alive today. The most likely scenario, says Peterson, is that they were a primitive type of animal with fungus-like traits that left no living ancestors. Narbonne and Gehling agree. "The rangeomorphs were a failed experiment in animal evolution," says Narbonne. "They were not ancestral to anything in the present world."

Why did rangeomorphs evolve when they did? For 3 billion years life had been mainly microbial. What changed to make large, complex designs so desirable? The key may lie in the fact that, just 2 million years before the ›

rangeomorphs appear, Earth emerged from the last major ice age of the Precambrian. The Gaskiers glaciation closed a period known as Snowball Earth, when much of the planet froze over. Afterwards, there was a massive increase in deep-sea oxygen levels. "Things are getting big, and the rise in oxygen has to be key to this," says Gehling.

Peterson argues further that the primeval ocean would have been bursting with dissolved organic matter freed up by melting glaciers, which the rangeomorphs may have absorbed through their body surface. "Dissolved organic matter is concentrated in deep water where Ediacarans are feeding," says Gehling. Their fractal, modular design maximised their surface area, so was an efficient way of mopping up this sudden burst of plenty.

Their fractal construction may also have been what allowed them to grow so big. The rangeomorphs were small units writ large through fractal repetition, and that process may have been quite straightforward. A simple genetic switch may have been all that was required for tiny frondlets to iterate themselves into 2-metre giants. New research shows that the ability of the Ediacarans to grow upwards from the sea floor gave them an advantage over the microbes they were competing against for food. "This may explain the abrupt appearance of the Ediacara biota after 3 billion years of mostly microbial evolution," says Narbonne.

"Things are getting big, and the rise in oxygen has to be key to this"

PALEOBASE

***Charnia masoni*, discovered nearly 60 years ago, has a fractal structure and is one of the earliest Ediacarans to have evolved**

Conquering the shallows

The rangeomorph design remained a winning strategy for 20 million years but it appears to have had a major drawback: it worked best in the deep sea. Shallow-water rangeomorphs dating to around 550 million years ago have been found in Russia's White Sea and in Namibia, and "locally could be quite abundant," says Narbonne. "But on a global scale they are just a shadow of their former greatness."

The biological relationship between the rangeomorphs and the new, shallow-water Ediacarans is highly uncertain. What is clear is that the appearance of shallow-water Ediacarans marks the beginning of a golden age. For 10 million years, biodiversity was at a peak. "It was brimming with life," says Mary Droser of the University of California, Riverside. "We have bedding planes that are absolutely covered – wall-to-wall fossils."

The most spectacular shallow-water Ediacarans are known as the White Sea assemblage, and include fossils such as *Dickinsonia*, a flatworm-like creature that reached up to a metre in length, and *Tribrachidium*, a 2.5-centimetre disc topped with three spiralling arms – one of the most enigmatic of all the Ediacarans. Another is *Spriggina*, regarded by some palaeontologists as either a type of worm or an early crustacean, though this has been hotly disputed by others. There's also the mollusc-like *Kimberella*, which may have been among the first motile animals.

Even amid all this evolutionary innovation, the rangeomorphs clung on. There are some in an Australian group from 555 million years ago, though they are rare and are found only in the remains of deep-water canyons alongside rocks laid down in shallow waters. Their species composition is similar to the Avalon group. "There are almost two worlds in parallel," says Gehling.

In one of those worlds, pivotal evolutionary events were unfolding. Most of the well-known shallow-water Ediacarans were large and immobile and have no clear link to the creatures of the Cambrian. However, work by Gehling and Droser hints at the beginnings of the Cambrian explosion in a hitherto neglected group of small Ediacarans, 1 to 10 centimetres in length. One of these, *Parvancorina*, bears a close resemblance to an early Cambrian arthropod called *Skania*. Another, *Arkarua*, looks a lot like a Cambrian echinoderm, the group represented today by starfish and sea urchins.

This idea is backed up by recent research showing that skeletons and hard body parts – traits thought to have evolved in the Cambrian – were present in Ediacarans. For example, in 2012 the discovery was reported of the oldest animal with a skeleton, the sponge-like *Coronacollina acula* with tri-radial symmetry. It lived around 550 million years ago – as did the cup-with-a-stalk shaped animals called *Namacalathus hermanastes*, which also had calcium carbonate skeletons. Like the mammals that coexisted with dinosaurs, it appears that some small Ediacarans went on to inherit the Earth. The Cambrian explosion had a long fuse after all.

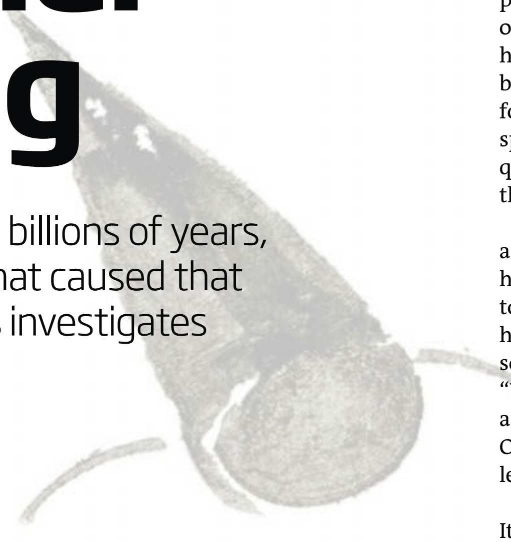
Unfortunately, a definitive verdict on the link between the Ediacarans and the Cambrian will be hard to reach. The fossil record tells us little about the final few million years of the Ediacaran period. Late Ediacarans are best known from Namibia, and range from 549 to 541 million years old. These are all shallow-water dwellers. They include frond-like forms such as *Pteridinium* and *Swartpuntia*, and the coral-like *Cloudina*; all are difficult to place on the tree of life.

Intriguingly, the Namibian group includes a shallow-water rangeomorph, *Rangea*. This conquest of the shallows was short-lived, though. The rangeomorphs disappear altogether about 541 million years ago, probably doomed by their own limitations. As long as organic nutrients were freely available, the rangeomorphs had no problem. But towards the end of the Precambrian, as this food supply became depleted by all the creatures now eating it, they ran into trouble. They were up against far more efficient feeders that drove them to extinction.

A handful of Ediacarans crossed over into the early Cambrian, including *Swartpuntia*. The overwhelming majority did not make it, though; the few that did vanished within 5 million years. The first great experiment in complex, multicellular life was over. But we now know it laid the foundation for everything that followed. ■

ROM/ZAK ROGERS

The other big bang



It was simple and boring for billions of years, then BOOM! life took off. What caused that dramatic shift? **Bob Holmes** investigates

THE "tink, tink" of chisel on rock echoes across the valley. High up in the Rocky Mountains of Canada, half a dozen palaeontologists are patiently splitting chunks of shale. Sunburnt, covered in rock dust, with hands blistered from their labours, they have been living rough here near Marble Canyon for four weeks now. The season is short, and they spend almost every daylight hour at the quarry, a rock face about 4 metres deep. But their efforts are paying off.

Before long, a block falls open to reveal an almost perfectly preserved arthropod from half a billion years ago – a distant cousin of today's insects and crustaceans. Hour after hour, the finds continue – more than 3000 so far. And the richest strata are yet to come. "We are expecting an amazing array of new animals," says Jean-Bernard Caron of the Royal Ontario Museum in Toronto, Canada, who leads the project.

Marble Canyon was only discovered in 2012. It is part of the famous Burgess Shale, perhaps the richest source of information about early animal life on Earth. The tale the shale tells is one of a sudden, dramatic burst of animal

Excavations at Marble Canyon in Kootenay National Park, Canada, are revealing fossils of animals that lived half a billion years ago, during evolution's equivalent of the Italian Renaissance

BOTH ROM/JEAN-BERNARD CARON

diversification known as the Cambrian explosion, evolution's equivalent of the Italian Renaissance. These creatures are so bizarre-looking that 27 years ago, palaeontologist Stephen Jay Gould argued in his book *Wonderful Life* that they represent a failed experiment that left few descendants in today's world. Since then, most of the Burgess fauna have been recognised as members of modern animal groups – albeit odd, experimental ones. That means that in just a few tens of millions of years – a geological instant – almost every major animal group we know made its first appearance in the fossil record, and the ecology of the planet was transformed forever.

The original Burgess Shale in Canada's Yoho National Park was discovered over a century ago, and has yielded some 200 animal species to date. Marble Canyon looks set to surpass even this, and in 2014 Caron's team reported that some of the creatures they found there match those in China's Chengjiang fossil beds, suggesting that some Cambrian species had a worldwide distribution.

Scientists have struggled to explain what sparked this sudden burst of innovation. Until recently, most efforts tried to find a single trigger, but over the past year or two, a different explanation has begun to emerge. The Cambrian explosion appears to have been life's equivalent of the perfect storm. Instead of one trigger, there was a whole array of them amplifying one another to generate a hotbed of animal evolution the likes of which the world has never seen before or since.

Even without these particularly striking fossils, it is clear that something dramatic happened at the beginning of the Cambrian period, 542 million years ago. For most of the 3 billion years before then, life was unicellular. The first sign of multicellular animals is in rocks about 750 million years old, which contain fossilised biomolecules found today only in sponges. Then another 150 million apparently uneventful years passed before the appearance of the Ediacaran fauna (see "Life's long fuse", page 36). This enigmatic group of multicellular organisms of uncertain affinities to other lifeforms flourished in the oceans up to the beginning of the Cambrian. Then all hell broke loose.

"Something happened, right at the base of the Cambrian," says Caron. Most Ediacarans vanished abruptly, in what may have been the first mass extinction. What took their place is a mystery because we have few whole-animal fossils from the earliest part of this period. But trace fossils – the preserved remnants of burrows, tracks and the like – clearly show that big changes were happening.

Throughout the Ediacaran period burrows were simple, barely more than shallow trenches ploughed in the seafloor. Palaeontologists can pick out seven distinct types, which they assume correspond to a few different body forms – grazing worms, actively foraging worms, suspension-feeding worms and surface-scratching mollusc-like animals. At the beginning of the Cambrian, that number abruptly jumped to 22.

"In terms of basic forms, you have tripled, very quickly. That is a huge thing," says Gabriela Mangano at the University of Saskatchewan in Saskatoon, Canada. The trace fossils from this time include burrows of all different kinds: deep, vertical, meandering, U-shaped – even burrows that wind back ›

and forth, systematically exploring a patch of ground. At the same time, fragments of fossilised shells, spines and other hard body parts become much more abundant. These indicate that a diverse set of animals evolved early in the Cambrian.

By the time the first whole-body fossils turn up, in shales from about 520 million years ago, almost all the major groups of animals are already present. In other words, virtually all modern groups seem to have originated between about 540 and 520 million years ago. "You go from seemingly nothing to everything in a few million years," says Kevin Peterson, a molecular palaeobiologist at Dartmouth College in New Hampshire.

Why did this sudden burst of evolution happen when it did? One possibility is it simply took that long for animals to evolve the genetic toolkit necessary to build themselves into complex, mobile forms. "In my mind, 200 million years to figure out all the body plans and get things going seems about right," says Nick Butterfield, a palaeontologist at the University of Cambridge. He describes the

"Like any good mystery, the Cambrian explosion has several key suspects"

gene networks that control development from an egg into a multicellular animal as the most complex algorithms ever developed. "At some stage, everything's going to line up and take off. I call that the Cambrian explosion."

But that explanation may be too simple. Studies of "molecular clocks" – which use the gradual accumulation of genetic changes to estimate when particular evolutionary branches diverged – suggest that animal complexity emerged before the Cambrian. For example, humans and starfish have a common ancestor back in the Ediacaran period, implying that the shared details of their biology – including body cavities, guts, nervous systems and more – must have been present then, too. "Developmentally, everything's there long before the Cambrian," says Peterson.

So why didn't the Cambrian explosion happen earlier? If the genetic toolkit was in place, why the lag? "It's necessary, but not sufficient. It's not driving," says Douglas Erwin at the Smithsonian National Museum of Natural History in Washington DC. In other words, other triggers were required. He points to two huge ecological innovations that make their debut in the Cambrian fossil record.

The first is the ability to burrow into the sea floor. These burrows would have broken up the stagnant microbial mats that dominated the Ediacaran sea floor and brought oxygenated water down into the sediment, stimulating productivity. "By ventilating the sediment, you're basically producing food," says Erwin. The many kinds of burrows also make for a more complex environment, so that animals have a wider range of ways to make a living.

The second innovation was predation. The beginning of the Cambrian features the first examples in the fossil record of true predators – animals that catch and eat other animals. "I don't think that's a coincidence," says Peterson. With predation comes a much richer and more intense set of evolutionary pressures, as predators and their prey get caught up in "arms races". This spurs the development of faster-moving animals, hard-bodied prey, stronger predators, better burrowers, sharper sense organs and the like.

Taken together, these probably led to an evolutionary snowball effect, as one original design begat another and diversity begat greater diversity – leading, within a few million years, to the profusion of new body plans and lifestyles evident in Caron's Marble Canyon fossils. In effect, the rapidly evolving animals of the Cambrian were inventing whole ecologies on the fly, says Erwin.

Such a burst of creativity would be unlikely in today's world, which is already teeming with animals of all sorts and sizes. But the ecologically sparse Cambrian world would have presented less competition, allowing animals to work out the "growing pains" that are inevitable with any radical redesign. Erwin points out that you see similar evolutionary experimentation after mass extinctions. For example, the great Permian extinction 252 million years ago, in which over 90 per cent of all species became extinct, was followed by a spate of innovation in vertebrate form that led to the dinosaurs, turtles and others.

This case for an ecological trigger has been

around for several years, but it still doesn't explain the exact timing of the animal explosion. What sparked the key innovations that were needed for a biological boom? What else were these early creatures waiting for?

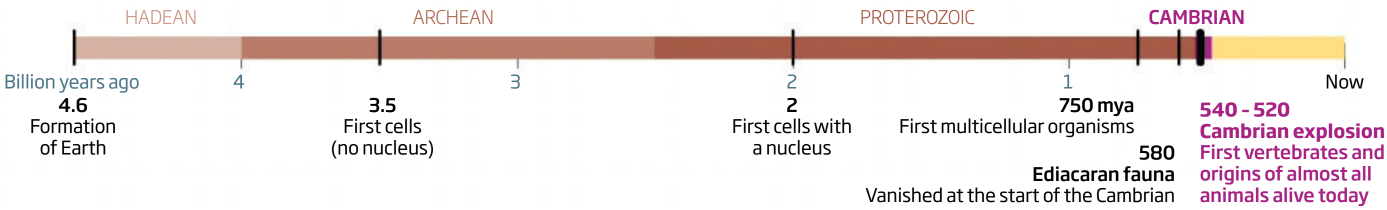
Fantastic fertiliser

One intriguing possibility is that they were waiting for fertiliser. Geological evidence suggests that rising sea levels during the Cambrian could have increased erosion, boosting levels of nutrients such as calcium, phosphate and potassium in the oceans. This fertilisation would have sparked an increase in productivity, providing more resources, generating longer, more intricate food chains and allowing the ecological positive feedbacks to take off.

But there's a problem with this idea. "Nutrients alone don't tell you how you get increases in ecological complexity and diversity," says Erwin. "If you put nutrients into an ecosystem today, what you get is a huge increase in abundance of a small number of species." Today's polar oceans, for example, are among the most productive

A long time coming

For almost as long as the planet has existed, there's been some kind of life on Earth. Yet it stayed much the same for 3 billion years before suddenly exploding into variety



ROM/JEAN-BERNARD CARON

BOTH, ROM/ JEAN-BERNARD CARON

Marble Canyon has yielded more than 80 animal species so far, including sponges (top) and arthropods (below). Bottom: the Marble Canyon camp

and least diverse marine ecosystems.

Nevertheless, calcium was key for one Cambrian innovation: high levels dissolved in the oceans, combined with carbonate ions, would have made it easier for animals to form hard shells and skeletons, helping spark the ecological arms race. In fact, these high calcium levels might even be the reason the Burgess Shale fossils are so well preserved. But most species that appear in the Cambrian explosion are entirely soft-bodied. "What about the rest of the animals?" says Caron. Some further ingredient is needed.

One likely candidate is oxygen. For most of Earth's history, oxygen gas was exceedingly rare. A study published in 2015 concluded that until 800 million years ago, oxygen levels were less than 0.1 per cent of present levels, which would have precluded any sort of active animal life. Atmospheric oxygen levels crept up gradually after that. And although geochemists do not yet agree on the specifics, at some stage oxygen levels in the oceans would have risen to the point where active, predatory lifestyles became possible.

To learn more about where this point was, Erik Sperling at Stanford University and his colleagues looked to modern sea floor habitats. Sure enough, sites that were almost devoid of oxygen had very few predators, while those with more oxygen supported more diverse communities of predators, they reported in 2013. The crucial threshold seemed to be between 1 and 5 per cent of present oxygen levels. Geochemists' best guess at when the ancient oceans reached this point is about 550 million years ago – just in time to kick off predation and its resulting ecological feedback. "That's about what you'd expect if oxygenation was a trigger for the Cambrian explosion," says Sperling.

Most biologists think that photosynthetic plankton were responsible for the gradual increase in oxygen. Two years ago, however, a few researchers argued that animals may have had a hand in fashioning the trigger, too. The idea, proposed by Butterfield, goes like this: Precambrian oceans were full of single-celled algae and bacteria. When these small cells died, they would have started to sink, decomposing quickly as they went – and because decomposition consumes oxygen, this would have kept ocean waters anoxic. Filter-feeding sponges, which evolved sometime before the Ediacaran,then started clearing these cells out of the water column before they died and decomposed. The sponges themselves, being larger, were more likely to be buried in the sediment after death, allowing oxygen to remain in the water. Over time, this would have led ever more of the ocean to become oxygenated. "The sponges basically march from shallower to deeper water, oxygenating as they go," says Erwin.

Like any good mystery, the Cambrian explosion has several prominent suspects. It is becoming increasingly clear that they worked together, but we still don't know exactly how. "It's very difficult to separate what are the triggers and what are the consequences," says Caron. Nevertheless, as palaeontologists find more fossils, and develop more techniques for inferring past environments from geological clues, the answers may emerge quickly. "There are so many really good people working on this," says Erwin. "It's amazing how fast things are changing."

Caron and his team at Marble Canyon are in the vanguard of this progress. In just three short excavation seasons they found tens of thousands of fossils from at least 80 species, some of them never seen before. They also discovered several new outcrops which they will begin excavating this summer.

Their finds will shed more light on the perfect storm of factors behind the Cambrian explosion, but Caron still can't resist wondering what sparked the storm. "I think that's the million-dollar question," he says. And occasionally he worries there may be no way of knowing. "It's possible that what we're looking at here is a random event." ■

ROM/ ZAK ROGERS

THE SECOND COMING

The Cambrian explosion was big. But what came next was the truly momentous event in animal evolution, says James O'Donoghue


PETRA BORNER

JUST over half a billion years ago, evolution hit a purple patch. In the space of a few million years, once-empty seas were suddenly overrun by all manner of newfangled life forms. Animals had arrived on the scene and life on Earth never looked back.

At least, that's what we originally thought the fossil record was telling us. It now turns out that this spectacular event – known as the Cambrian explosion – stuttered to a halt not long after it began. Around 515 million years ago, evolution ran out of steam and the increase in biodiversity went into reverse. For the march of progress to continue, life needed rebooting.

It came in the form of a second explosion of life called the Great Ordovician Biodiversification Event, a little-heard-of episode which has been the focus of intense scientific interest in recent years. Since discovering hints of it around 30 years ago, palaeontologists have established beyond doubt that the "Ordovician explosion" was every bit as momentous for animal evolution as the Cambrian one. Now they are asking a more difficult question: what caused it?

The Cambrian period, from 542 to 489 million years ago, has always exerted an irresistible lure for palaeontologists. For thousands of millions of years before it, the most complex life forms on Earth were marine microbial mats known as stromatolites. These were briefly superseded by the enigmatic Ediacarans, the first large-bodied life forms on Earth – and it is possible that simple animals such as sponges were around even earlier. Then, in the space of just 20 million years at the start of the Cambrian, all bar one of the basic types, or phyla, of animals we see around us today, made their appearance in the fossil record.

Stromatolites became lunch and faded away as trilobites and other arthropods came to dominate the seas. High levels of dissolved nutrients supported filter-feeders such as sponges, molluscs, echinoderms and clam-like brachiopods. Diverse reef systems formed around stony sponges called archaeocyathids.

But this watery Eden wasn't to last. The fossil record reveals a decline in biodiversity by the middle of the Cambrian, one so steep that in the early 1990s Phil Signor, then at the University of California, Davis, suggested there had been a mass extinction starting around 515 million years ago.

It later became clear that the decline in biodiversity was not a mass extinction but resulted from a sharp drop in origination – the rate at which new species appear. By the mid-Cambrian the origination rate in many groups had fallen to between a fifth and a third of the levels seen earlier, well below the natural rate at which species were becoming extinct. It's not clear why this happened, but the result was a decline in biodiversity. Many groups were hit hard, while the archaeocyathids disappeared altogether and were replaced by stromatolites. Cambrian life had gone from explosion to damp squib.

By 510 million years ago, the number of genera had dropped to 450 from a peak of about 600. "The middle to late Cambrian is almost like an empty quarter. There is a surprising amount of barrenness," says Arnie Miller, a palaeobiologist at the University of Cincinnati in Ohio.

Then, at the start of the Ordovician period, 489 million years ago, evolution sparked back into life. First came massive algal blooms, which provided a bountiful food supply for filter-feeders, kick-starting an evolutionary bonanza. The stromatolites were booted out once more, with sponges re-establishing themselves as major reef-building organisms. They were joined by coral species as reefs again became hotspots of biodiversity (see "Life in the Ordovician seas", page 49).

The evolutionary tempo picked up and new animal species began to appear as never before.

Though only one new phylum appeared during the Ordovician – the moss animals or bryozoans – diversity within existing phyla rocketed, quickly outstripping anything achieved in the Cambrian. “During the Cambrian there is a fantastic array of new body plans, but it wasn’t until the early to mid-Ordovician that we got a really striking increase in diversity,” says Dave Harper of the University of Durham, UK. By the end of the Ordovician, biodiversity had reached a level that would not be surpassed for another 200 million years. Look along the shoreline today and chances are you will find creatures that first appeared in the Ordovician, including starfish, sea urchins, oysters and scallops.

The Ordovician also saw an increase in ecological complexity. During the Cambrian, animals had largely been confined to the sea floor. There may have been a few worms poking around in the mud and the odd animal in the water immediately above, but the real action was on the sediment itself. That largely two-dimensional world was fundamentally altered by the Ordovician newcomers. Burrowing animals went deeper than before, churning up the sea floor and creating new habitats. “You are pushing more and more species into the same space, and they are having to start to do things in a different way,” says Harper. “One of the ways is to dig deeper and deeper, but they are also building higher and higher tiers [of reefs] above the sediment.”

“In the Ordovician, new animal species began to appear as never before”

As competition increased, more ingenuity was required to survive. Whereas filter-feeders once sat back and waited for food to arrive on the currents, they were now having to actively filter the water for nutrients. Another way to survive was to escape the sea floor altogether. By the mid-Ordovician the larvae of several different animal groups had developed the ability to swim away from the sea bottom. This may have been driven by the need to dodge the swaying tentacles of the filter-feeders.

Life also staked a greater claim on land. Simple plants colonised damp areas, while scorpion-like eurypterids took their first tentative steps along the shoreline.

This boom was like nothing the world has seen since. The Ordovician is the only time in the history of animal life that huge numbers of new species appeared without a mass extinction to clear the decks beforehand. “It’s a real enigma in the history of life, ›

and from my perspective it's unique," says Mary Droser, a palaeobiologist at the University of California, Riverside.

So what triggered it? "There isn't a simple, sexy explanation," Droser says. One possibility is that there was no evolutionary need to clear the decks: the stalled Cambrian explosion had left plenty of ecological space to be filled.

It's certainly clear that environmental and geological conditions during the Ordovician were especially suited to biodiversification, says Alan Owen of the University of Glasgow, UK. "It was a time when the Earth's continents were widely dispersed and of extreme provincialism," he says (see maps, below). "The seas around each continent had their own fauna. It was a time of mountain-building, which generated uplift, erosion and the introduction of nutrients into the sea. It was also a time of intense volcanic activity which generated yet more nutrients and created local environments where things could evolve."

The climate played a key role, too. The surge in biodiversity in the Ordovician was once thought to have coincided with a warm, stable climate. However, new research led by Christian Rasmussen of the Natural History Museum of Denmark shows that this explosion of life in fact occurred at the same time as a sudden temperature drop, with the sea floor cooling by at least 5 °C. Prior to this, in the late Cambrian, sea surface temperatures were perhaps higher than 40 °C, hindering the ability of life to evolve and diversify. The cooling may have allowed a huge ocean circulation system to develop, bringing nutrient-rich water up to the surface and boosting oxygen concentrations. Rasmussen thinks this initiated a revolution for the entire ecosystem.

Sea levels were also some of the highest the world has ever seen, covering continental shelves with great expanses of shallow water that provided light, oxygen and nutrients for life to thrive in. "There are no modern analogues for these very big, broad, shallow water areas," says Miller. "That sort of sea does not really exist now."

There is no doubt that these general environmental triggers boosted biodiversity in the Ordivician. But Birger Schmitz, a geologist at the University of Lund in Sweden, goes further, suggesting that there could indeed be a simple, sexy explanation for the diversity boom: the Ordovician explosion may have been triggered from space.

Asteroid impacts are usually seen as the harbingers of doom, bringing death and destruction. Not so for Schmitz. He argues that colossal impacts during the Ordovician created the conditions for biodiversification, and believes he has evidence to prove it.

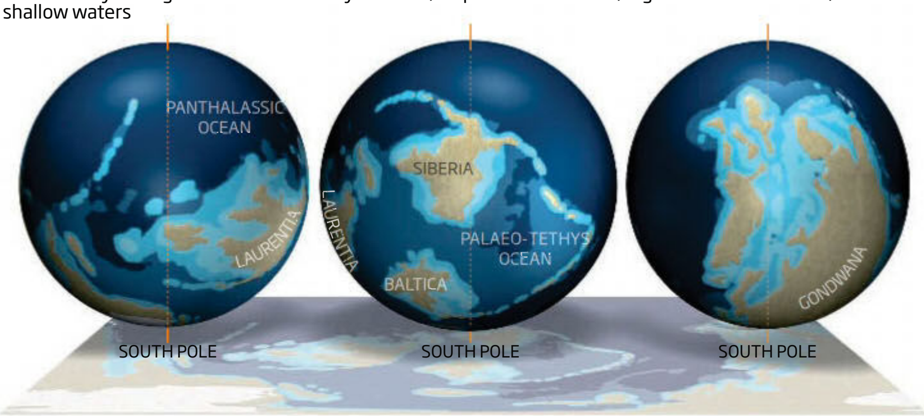
The story begins 470 million years ago, when a large asteroid broke up in the solar system, creating a swarm of smaller asteroids and meteoroids. Most of the fragments are still out there and, even now, they make up the majority of meteorites that fall to Earth.

"If you are going to be hit by a meteorite, the probability is it will have an age of 470 million years," says Schmitz. The only confirmed case of a human being hit by a meteorite was when a young boy was struck by a fragment of this asteroid in Uganda in 1992. Luckily it didn't do him any harm.

The same probably could not be said of Earth in the period immediately after the asteroid break-up. In 1988, Jan Nyström of the Swedish Museum Of Natural History in Stockholm announced a rare find – a fossil meteorite embedded in a slab of mid-

The middle Ordovician Earth

470 million years ago was a time of balmy climates, dispersed continents, high sea level and warm, shallow waters



Ordovician limestone from the Österplana quarry in Kinnekulle nature reserve, Sweden. Since then, around 100 beautifully preserved fossil meteorites have been found in the area. Dating studies showed that these crash-landed into the Ordovician sea 467 million years ago, where they came to rest on the sediment and were fossilised alongside Ordovician creatures.

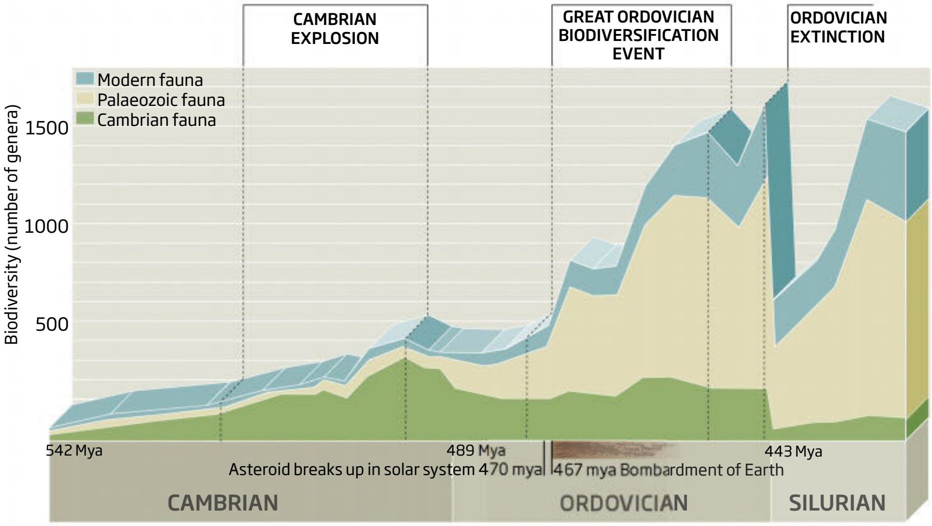
Fossil meteorites are very rare, but ancient impacts leave other traces which can be detected in sedimentary rocks, in the form of grains of the mineral chromite found in extraterrestrial material. Schmitz uncovered this in abundance in mid-Ordovician strata throughout Sweden and also in China, then – as now – several thousand kilometres away.

Based on the abundance of fossil meteorites and chromite in mid-Ordovician rocks, Schmitz concluded that the rate of impacts was around 100 times what it is today. And if meteorites were raining down thick and fast then enormous, destructive asteroids could not have been far behind, he says. This theory is backed up by the relative abundance of Ordovician impact craters among the 170 or so known craters on Earth, which suggests that large impacts were more common by a factor of 5 to 10 during the Middle Ordovician than at any other time in the past 540 million years.

Could this be linked to the biological events that were unfolding at the time? Both Schmitz and Harper think so. Between 2000 and 2002, Harper and his team compiled a detailed record of fossil brachiopods – the most abundant and diverse animals of the Ordovician – in western Russia, Sweden, Norway and Estonia, all part of the region geologists call Balto-Scandinavia. This

Life's big events

The Cambrian "explosion" looks positively weedy in comparison with what happened in the Ordovician



SOURCE: NATURE GEOSCIENCE, VOL1, P 49

revealed a sudden rise in biodiversity around 467 million years ago, just as the area was being bombarded. "It matches the asteroid data more or less precisely," says Harper.

Schmitz believes that the destruction wrought by asteroids might have created the right conditions for diversification. He speculates that in the early Ordovician, the occupants of the sea were both widely dispersed and generalists, unspecialised in their ecological preferences. The asteroid impacts would have caused localised extinctions and thus created lots of vacant ecological niches for life to evolve into.

Palaeontologists have given Schmitz's idea a cautious welcome. "It's an intriguing idea and a lot more could be done to test it," says Miller. Lots more is being done – the trick now is to replicate the findings elsewhere. So far, Schmitz only has evidence of a link between impacts and diversification from one region, Balto-Scandinavia, and only in one group, the brachiopods. The Chinese chromite shows increased meteorite flux, but so far there isn't any fossil evidence to go with it.

The great biodiversification event was not to last indefinitely. A short-lived ice age, during the late Ordovician, coincided with a one-two extinction punch: the cold intensified and again brought major changes to ocean circulation, but unlike the mid-Ordovician cold spell, this killed off an estimated 85 per cent of all species. Sea levels dropped at least 100 metres, resulting in the loss of the shallow water habitats over continental shelves. When the ice melted, the oceans were flooded with poorly oxygenated water.

The rapid onset and decline of this ice age probably contributed to the extinction too – many life forms simply didn't have time to adapt when their habitats were also being destroyed by the amalgamation of continents. The mass extinction at the end of the Ordovician period, 443 million years ago, was one of the most devastating ever to hit the planet.

Fortunately, all was not lost. The arrival of so many new species and specialised ecosystems was not to be undone lightly. Life was now in much better shape to weather an extinction storm and bounced back fairly quickly. Diversity and complexity in the living world have stayed with us, the legacy of that long-ignored primeval boom. ■

Life in the Ordovician seas

Marine fauna thrived in the Ordovician. Most abundant were brachiopods - shelled creatures vaguely resembling clams - together with bushy colonies of bryozoans on the sea floor.

There were also flowery crinoids, sea urchins, corals, sponges, clams and snails. Planktonic graptolites, shaped like letters from a defunct alphabet, drifted in the water. The stars of the show, though, were the trilobites and the shelled cephalopods.

Most trilobites were just a few centimetres long but one predatory species, *Isotelus rex*, grew to up to 70 centimetres, well over half as big again as the next-largest trilobite.

There was also a tremendous diversity of cephalopods in all shapes and sizes: tightly or loosely coiled and straight or curly shelled. Many of these creatures were highly mobile, and formidable predators at the top of the food chain.

***Cameroceras*, which grew to up to 5 metres long, is one of the largest invertebrates ever to have lived.**

CHAPTER THREE

FOSSILS

Signs of early life

Fossils are not just petrified body parts such as bones and shells. They also include ancient bacteria and dinosaur footprints. Although only a tiny percentage of everything that has ever lived is fossilised, fossils are our most reliable indicator of the organisms and environments of the past. Pat Shipman is your guide

SINCLAIR STAMMERS/SPL, BACKGROUND PHOTOGRAPH ALAN SIRULNIKOFF/SPL

Staying power: trilobites evolved in the Cambrian and lasted for 270 million years

THE OLDEST REMAINS

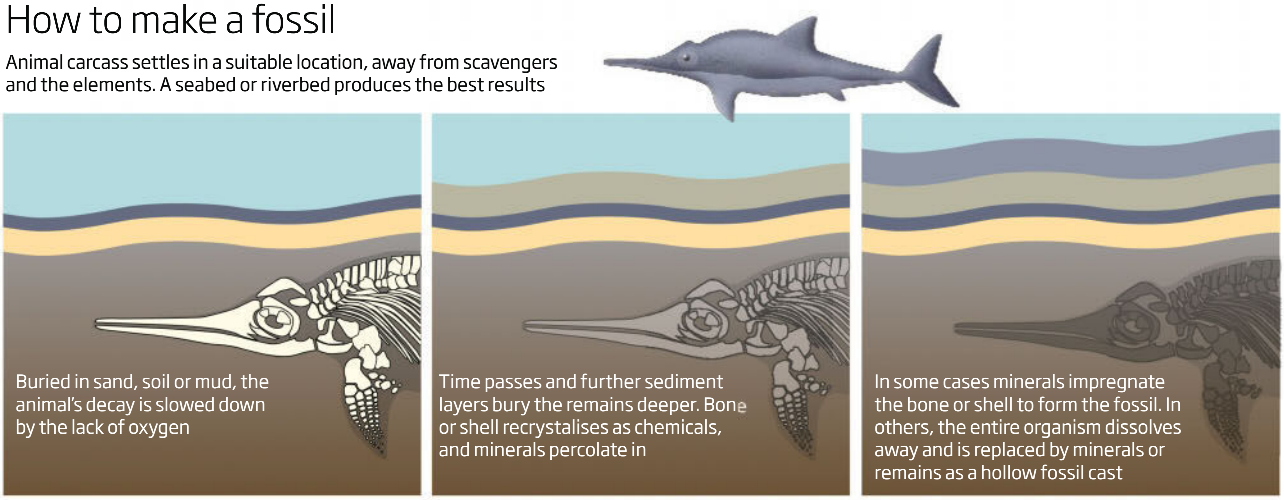
It is unlikely that the very first life on Earth became fossilised, but finding the oldest fossils that do exist could help solve the twin mysteries of when and how life began. This is a huge challenge, not least because the oldest life forms probably didn't resemble anything alive today. As a consequence, candidates for the title of first fossil are inevitably controversial, with sceptics suggesting they are merely strange geological formations rather than once-living organisms.

At present, the top contender is a collection of 3.4-billion-year-old microscopic blobs found in Strelley Pool, Western Australia, by David Wacey of the University of Western Australia and colleagues. Several lines of evidence suggest that these are biological rather than geological in origin. Since life on Earth is cellular, the oldest fossils ought to have regular cellular structures, and these blobs seem to fit the bill. Most are ovoid or spherical in shape, have hollow centres surrounded by what look like cell walls of a uniform thickness, and they fall into the size range of known microbial organisms.

The blobs also show indications of biological behaviour, says the team. They are confined to a layer of rock comprising black sandstone rich in pyrite, suggesting the blobs have a preferred habitat. Some have what look like split cell walls, with the contents extruded, just as might be seen in a deteriorating cellular organism.

The walls themselves are rich in carbon, nitrogen and sulphur, suggesting that this early life had a metabolism based on sulphur. This finding is key, the team argue, because 3.4 billion years ago the world was hot and nearly oxygen-free, and volcanic activity would have led to an abundance of sulphur.

How to make a fossil



THE CAMBRIAN EXPLOSION

The strange world of the Ediacarans was followed by something even more bizarre. About 505 million years ago there was an explosion in biological diversity called the Cambrian (see "The other big bang", page 42). Fossils from this time are found in the Burgess Shale of the Canadian Rockies. This is a dark, almost black, mudstone that formed on the ocean floor and the fossils are found in films that can best be seen by tilting the rocks in the light. Exactly how they were preserved is a mystery. All the fossils are flattened and some seem to have been broken up by churning of the sediments.

Many Burgess Shale species used filter feeding to extract organic matter from the muddy sea floor or from the ocean waters, but about 10 per cent were predators of weird design. One, *Anomalocaris*, was up to 70 centimetres long. It was originally thought to be three separate organisms: its arm or feeding appendage was taken to be a shrimp-like creature, the mouth was classified as a jellyfish and the body as a sponge. This misinterpretation arose partly because no one expected to find such a large creature and partly because *Anomalocaris* had both hard and soft body parts, which preserved differently and often became separated. The truth was revealed when a specimen with an unmistakable connection between arm and mouth was found.

Another famous Burgess Shale specimen, *Hallucigenia*, is so peculiar that it is unclear where the head is or even which way up it goes. Named for its "bizarre and dream-like quality" by Simon Conway Morris from the University of Cambridge, it is believed to be related to arthropods – crabs, spiders and the like. Originally, Conway Morris reconstructed the creature as a sort of worm that walked on seven pairs of jointed spines and grasped food with a set of seven large tentacles and three pairs of smaller ones, all on its back. These days, most people flip the creature over, so that it walks on paired tentacles and is protected by spiny armour. Either way *Hallucigenia* is a very odd animal.

EDIACARAN FAUNA

The earliest fossils of recognisable multicellular organisms formed about 585 million years ago – long after the oldest fossils. Named after the Ediacaran Hills in Australia where they were first identified, these animals were oxygen-dependent, so could only have evolved after photosynthesising microbes had transformed the early, sulphur-rich atmosphere into one rich in oxygen.

Ediacaran fossils have been found on all continents except Antarctica, suggesting they inhabited oceans worldwide. Because these animals were soft-bodied, their fossilisation is something of a puzzle. Fine-grained sediments and volcanic ash seem to be key; these sediments are held together by the sticky secretions of microbial mats, which may have cushioned the delicate bodies. The fossils range from a few millimetres across to metres in length and are so unusual in form that their identification as animals is sometimes debated. One, *Charnia*, could be loosely described as a fried egg with a feather or fern-like appendage. Another, *Dicksonia constata*, looks like a squashed, quilted bag. Others look more familiar, resembling sea pens, primitive jellyfish and sea squirts. What is indisputable is that they were highly complex, multicelled creatures (see "Life's long fuse", page 36).

The demise of the Ediacaran fauna came at the start of the Cambrian period, around 542 million years ago. No one knows why they disappeared. Temperature fluctuations and changes in ocean and atmospheric chemistry have been suggested, as has the break-up of the supercontinents and the evolution of predatory organisms.

Disc world: *Tribrachidium heraldicum*'s three arms are rare in the animal kingdom

FRANS LANTING/CORBIS

Not just bones and stones

Fossilisation involves the consolidation of sediments under pressure and the replacement of organic material by minerals. Most tissues disintegrate before these processes can occur, which is why it is rare to find intact organisms and fossilised soft tissues.

COLOURING IN THE PAST

In 2008, graduate student Jakob Vinther, then at Yale University made an extraordinary discovery. He found that you can reconstruct the colour and patterning on the feathers of ancient birds and dinosaurs by looking at the shape of the fossils' pigment organelles, called melanosomes. These may contain melanin, which creates black pigmentation – or, in its absence, white – or other pigments that produce greys, rusty reds, browns, yellows, oranges, greens and blues. Each pigment gives the melanosome a distinctive shape. The arrangement of the pigments within a feather refracts light, generating colours or iridescence like that found in starlings and hummingbirds.

The first feathered dinosaur to be coloured in this way was a 150-million-year-old *Anchiornis huxleyi* from Liaoning province in China. When a team led by Vinther and Li Quanguo of China University of Geosciences, Beijing, examined samples of the fossilised feathers under a scanning electron microscope, they discovered that the animal was extravagantly coloured, with spots, stripes and a red crest of feathers down its skull. Such dazzling colour could have been used to attract mates, the team suggest.

Show piece: was *Anchiornis huxleyi* trying to attract a mate?

Minute detail: armoured Jurassic fish in the fine limestone at Solnhofen

JONATHAN BLAIR/CORBIS; RIGHT: MIKE SEGAR/REUTERS; ABOVE: IMAGINECHINA/CORBIS

MAMMALS AND MORE

One of the most exciting sites is in Messel, Germany. Here, fine-grained rocks preserve a 47-million-year-old ecosystem in exquisite detail, including some animals that are rarely fossilised, such as the earliest pangolin, bats, anteaters and insects. Many of these fossils come complete with stomach contents, fur and skin alongside the hard parts more commonly preserved, such as skeletons, beaks and teeth. In 1995 this site was declared a UNESCO World Heritage site of exceptional importance to palaeontology.

The variety of life preserved at Messel is staggering and includes fish, snakes, lizards, crocodiles and alligators, birds, two types of early horse and some of the first carnivores. In 2009, an extraordinary primate fossil was added to the list. Although not the ancestor of all humans as first suggested, *Darwinius masillae*, nicknamed Ida, is important as a very early higher primate similar to modern lemurs.

The extraordinary preservation at Messel is down to the ancient environment. The landscape featured a lake surrounded by rainforests through which rivers wound, creating a wet habitat with lots of sedimentation. Periodically, the oxygen-deprived mud on the bottom of the lake was stirred up, releasing lethal carbon dioxide and killing many animals nearby. As at Solnhofen, Germany, these sediments were devoid of life, allowing organisms to fossilise rather than simply decay. All that remains today is a damp oil shale, which deteriorates as it dries. To preserve the fossils, the shale has to be delicately removed from one side, before a synthetic resin is added. This seeps into the bones and hardens them. The shale next to the fossil is then reinforced with a layer of lacquer, before the whole process is repeated on the other side.

Insulating fluff: a 130-million-year-old juvenile Dromaeosaur

EARLY BIRDS

Sites where soft tissues such as skin, muscles and internal organs are preserved are called *Lagerstätten*. One of the best known is at Solnhofen in Germany, where the pale, fine-grained limestone has been quarried since Roman times. It formed during the late Jurassic, some 151 million years ago, from sediments precipitated out of the water and onto the bottom of a shallow lagoon. Without currents to mix the salty water of the lagoon with that of the adjoining Tethys Sea, salinity rose and the sediment became devoid of oxygen – perfect conditions for preserving entire organisms. Any dead animal or plant that ended up in the sediment, whether falling in from the banks or sinking from the waters above, lay undisturbed by currents, scavengers and bacteria that cause decay.

The potential of the Solnhofen limestone as a fossil site was revealed in 1860 with the discovery of a fossilised feather, belonging to the first specimen of the earliest known bird, *Archaeopteryx lithographica*. Preserved alongside *Archaeopteryx* are thousands of other organisms. These include wonderful pterodactyls with their leathery, furry wings intact; a small running dinosaur called *Compsognathus*; marine crocodiles; insects including dragonflies and beetles; various fish; crustaceans such as horseshoe crabs; squid; jellyfish and plants.

"You can reconstruct the colour and patterning on the feathers of ancient birds and dinosaurs"

FEATHERED DINOSAURS

In the past two decades, Liaoning province in China has been one of the most important sites for fossil hunters. Many species new to science have been found here, but it is feathered dinosaurs, which date from between 130 and 120 million years ago, for which Liaoning is most famous. In 1996, photos of *Sinosauropteryx prima*, the first feathered dinosaur to be discovered, shocked the world by providing key evidence that birds evolved from dinosaurs. Since then, 30 species of feathered dinosaurs have been discovered, including juvenile specimens of *Tyrannosaurus rex*. Most come from Liaoning.

Fabulously detailed preservation reveals a range of feather types. Some specimens, including *Sinosauropteryx*, have hairy, unbranched fluff or proto-feathers. Others, like the oldest feathered dinosaur *Anchiornis*, have recognisable feathers but could not have flown because their wings were not large enough. Then there is *Microraptor gui*, which had four feathered wings, one on each limb. Despite putting models of this animal in wind tunnels, no one has been able to work out how it got around.

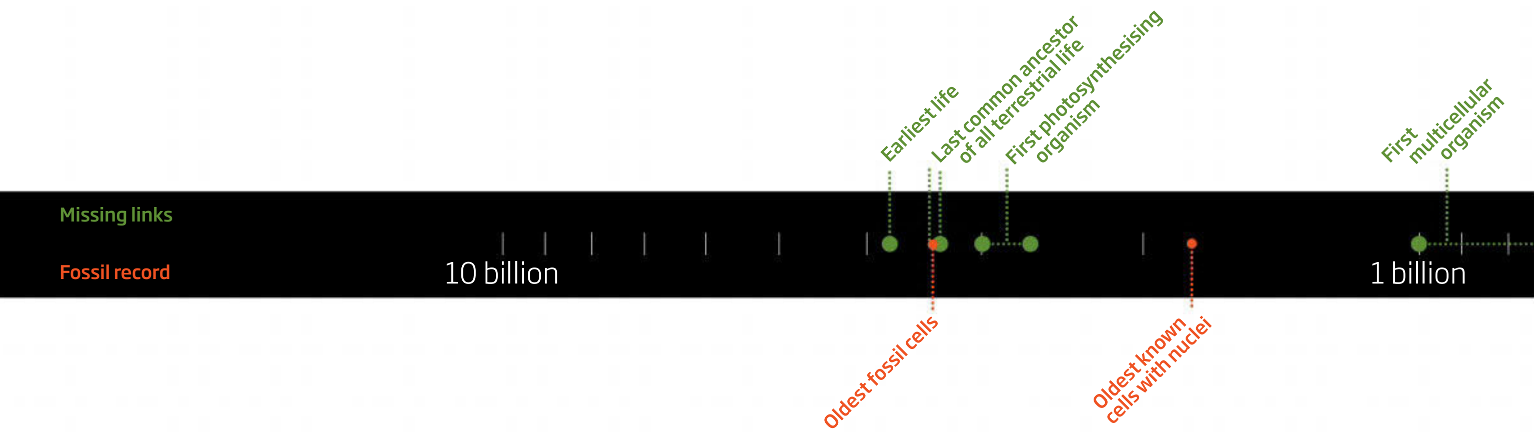
These fossils have forced us to consider that feathers evolved for a function other than flight. Possibilities include display, as some of the feathers were brightly coloured, and insulation against extreme heat or cold as in the Dromaeosaur (pictured).

"IT STARTS with a question," says Ted Daeschler. "What are the watershed moments in the history of life?" He is talking about evolution's most innovative twists – how birds took flight, when humans split from chimps, and how jaws originated, for example. To discover how these changes unfolded, we need what palaeontologists call transitional fossils – better known as missing links.

For Daeschler, who is based at the Academy of Natural Sciences in Philadelphia, Pennsylvania, the big question was: how did terrestrial animals evolve from fish? The key step, so we think, was when the lobe-shaped fins of some bony fish evolved into limbs around 375 million years ago. But there was no fossil evidence for this. So Daeschler teamed up with Neil Shubin from the University of Chicago and together they scoured geological maps in search of surface rocks of the correct age. Their spotlight fell on Ellesmere Island in the high Canadian Arctic and, in the fourth summer of digging,

Find the gaps

The hunt for evolution's missing links was always a haphazard affair. Now it is enjoying a very modern makeover, says **Jeff Hecht**



they finally uncovered their quarry: a fish with four limbs. They called it *Tiktaalik*.

When the discovery was announced in 2006, it made headlines around the world. People were captivated not only by the fossil, but also by how it had been found. In Darwin's day, naturalists collected anything of interest and many discoveries were made by chance. Daeschler's search was more systematic. "*Tiktaalik*," he says, "was a great example of a prediction that you could make and go out and validate" – by discovering the right fossil.

Today's missing-link hunters are increasingly taking such a tack, making predictions and then using a variety of advanced tools, ranging from gene sequencing to modern imaging techniques, to find the fossil evidence. It's an approach that is allowing palaeontologists to make big strides in understanding evolution's innovations all along life's timeline.

Life began well over 3 billion years ago; the ratio of carbon isotopes in 3.8-billion-year-old rocks from Greenland bears its fingerprint. But finding fossils from so far back is problematic. The very first link in the chain of evolution might not have fossilised and, even if it did, it could be unrecognisably different from anything alive today. Microscopic structures in Australian rocks 3.4 billion years old may be the oldest physical traces of life found to date. Not everyone is convinced.

However, thanks to genetic analysis, we are gaining important insights into another early transition. Rocks dating from about 2.4 billion years ago contain oxides of iron which signify the appearance of photosynthesising organisms that released oxygen. It has long been assumed that these organisms – known as cyanobacteria – originated in the sea. But when Carrine Blank of the University of Montana in Missoula sequenced the genomes of modern cyanobacteria to compile a family tree, she found strong evidence that all the ancestral species lived in fresh water. That suggests photosynthesis began in fresh water, probably between 3 and 2.5 billion years ago. Guided by this insight, Blank's colleagues are focusing on deposits from ancient lakes and streams in their search for fossil cyanobacteria.

The first photosynthesisers were single cells lacking a nucleus. Then came organisms with cell nuclei, the oldest known fossil of which dates from around 1.8 billion years ago. Evolution's next major trick was the emergence of multicellular life – a key missing link. Studies that use rates of genetic change to extrapolate backwards from today's creatures indicate that the first animals appeared between 1 billion and 600 million years ago. Fossils of that age are very rare, though, and even where they exist, it is difficult to distinguish between simple multicellular life and colonies of single-celled organisms.

The Ediacarans – mostly spongy, rippled mat-like creatures rooted to the seabed – emerged around 585 million years ago. They vanished abruptly 542 million years ago in a ›

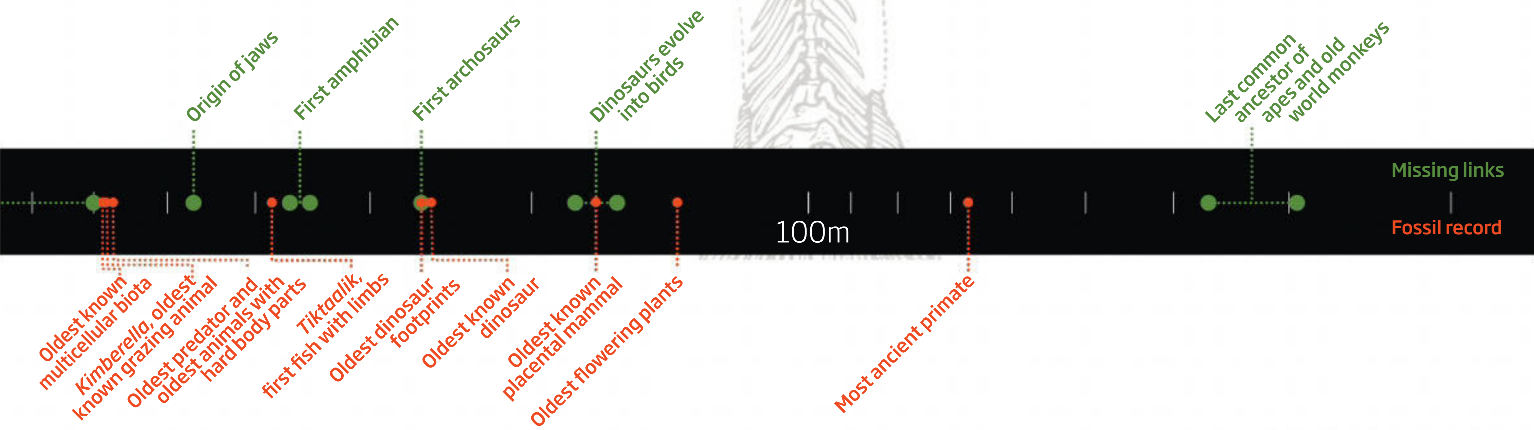
GETTY

burst of evolutionary change known as the Cambrian explosion. We can trace the origins of most major animal groups alive today to this period, which saw the evolution of the first animals with hard body parts, and the first predators. This transition changed the living world so profoundly that the evolutionary connections between Cambrian fauna and the Ediacarans remains an enigma.

Recent detective work has, however, shed light on a key innovation that happened in the seas around 100 million years later. "One of the biggest unsolved mysteries in evolution is the gap between jawless and jawed vertebrates," says John Long of Flinders University in Adelaide, South Australia. The evolution of jaws was vital to the success of species from sharks and *Tyrannosaurus rex* to humans. "It required a rearrangement of the

With limbs evolved from fins, *Tiktaalik* is a fish on the way to becoming an amphibian

TYLER KEILLOR



whole cranial anatomy," Long says. Now we know when and where that anatomical rearrangement got started. In 2011, Zhikun Gai at the Institute for Vertebrate Paleontology and Paleoanthropology in Beijing, China, announced that he had found a crucial intermediate form. He made the discovery using synchrotron X-ray microscopy, which gives 3D images at sub-micrometre resolution without damaging samples.

The specimen Gai scanned, that of a jawless fish called a galeaspid, had already been studied under optical microscopes, but the X-rays revealed something new hidden within the rock. Rather than the single nostril found in other jawless fish, Gai found a pair of nostrils, one on each side of the skull. In more advanced fish, the space between paired nostrils allows the embryonic cells that form jaws to migrate to the correct position. So although galeaspids remained jawless, by evolving paired nostrils they removed a barrier to jaw development.

ANCIENT POSTER CHILD

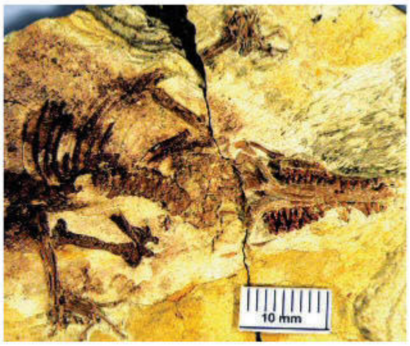
***Archaeopteryx* remains the iconic transitional fossil, a small predatory dinosaur caught in the act of evolving into a bird about 150 million years ago. Its discovery in 1861, just after publication of Darwin's *On the Origin of Species*, could not have been better timed. It would be another 130 years, however, before palaeontologists found a treasure trove of feathered dinosaurs and birds with similarly exquisite preservation. These fossils, at the Jehol formation in China, have raised a host of new questions about bird evolution, particularly how small dinosaurs evolved wings and flight feathers. However, they are some 20 million years younger than *Archaeopteryx*.**

Despite its fame, *Archaeopteryx* is rather late in the day as far as the shift from reptiles to birds is concerned. Researchers would really like to find transitional specimens that predate it, and were excited by the discovery a few years ago of older fossil beds beneath Jehol. Unfortunately the Daohugou formation has not lived up to expectations so far: it has yielded only about 20 species and no clearly identifiable birds, says David Hone of Queen Mary, University of London. The absence is a puzzle, but it's early days. Besides, the beds have yielded another key transitional fossil. At 160 million years old, *Juramaia sinensis* is the oldest known placental mammal, pushing the split with marsupials back 35 million years.

Archaeopteryx, the original missing link, was found by chance in a limestone quarry

Some 70 million years after this particular galeaspid swam the oceans, fish made another evolutionary leap when they took to life on land. *Tiktaalik* and its kin were the first fish with limbs strong enough to walk on the shore, but they were not proper residents. True amphibians evolved tens of millions of years later. Exactly how and when is hidden by a break in the fossil record called Romer's gap, named after the palaeontologist who first noticed it, Alfred Romer. Why fossil evidence from this period, from 360 to 345 million years ago, is so sparse is still debated, but we know that it followed a mass extinction at the end of the Devonian, the Hangenberg event, that wiped out many primitive fishes. Lobe-finned fish and the paddle-limbed descendant of *Tiktaalik*, *Acanthostega*, vanished. So did archaic armoured fish called placoderms, including the fearsome 10-metre-long *Dunkleosteus*. After the gap, more modern ray-finned fish and sharks dominated the seas, and amphibians with salamander-like legs roamed the land.

Recently, several fossil sites in the UK dating from Romer's gap were discovered. To fill in the gap properly, palaeontologists are undertaking an audacious project: drilling a borehole 500 metres deep through rocks



DR.ZHE-XI LOU/CARNEGIE MUSEUM OF NATURAL HISTORY


SALLY A. MORGAN; ECOSCENE/CORBIS

that include parts of these fossil beds. The idea is to obtain a core spanning the mysterious 15 million years. The TW:eed project, named after the drill site near the Tweed river on the border of Scotland and England, has uncovered at least a dozen new tetrapods – four-legged amphibians – which is impressive for a period where so little had been known. Details of these, plus other important findings, will be announced soon. Microfossils from the core will serve as an index that can be used to gauge the age of nearby fossil sites and how they relate to each other, potentially demystifying the rise of the amphibians.

Elsewhere, palaeontologists are making progress understanding the most devastating extinction of them all. Up to 96 per cent of all marine species and 70 per cent of terrestrial vertebrates died out in the end-Permian extinction, 252 million years ago. The next 20 million years saw the rise of the archosaurs, the "ruling reptiles" that gave rise to all birds, crocodiles, dinosaurs and pterosaurs. The first archosaur fossils appear at the start of the Triassic. Soon afterwards, the group seems to have split into lines leading to dinosaurs and crocodiles, and this is where things have been a little hazy. *Ctenosauriscus*, dating from around 247 million years ago, was only identified as an early relative of crocodiles in 2011. Footprints of a dinosaur or a dinosauromorph, its close cousin, found in Poland in 2010 are even older. But until very recently, the oldest known dinosaur fossil was just 230 million years old.

In 2012 a specimen some 10 to 15 million years older than that turned up. *Nyasasaurus* came as a surprise, not least because it had been sitting in the collection of the Natural History Museum in London for decades. Both it and *Ctenosauriscus* were identified as missing links thanks to a growing database of early archosaur specimens. With software to compare physical traits across many species, we can make connections not immediately obvious from skeletons. For example, *Ctenosauriscus* has a sail on its back, but computer analysis revealed many less obvious features that put it among the crocodilians. *Nyasasaurus* was spotted as a potential missing link by Sterling Nesbitt of Virginia Tech in Blacksburg, who does fieldwork at the Manda beds in Tanzania where it was unearthed. Sure enough, his computer-aided analysis revealed it to be an early dinosaur or close relative.

While looking for early birds, palaeontologists found the oldest known placental mammal

Nesbitt is also using a more commonplace tool that could have been a boon to past fossil hunters. Before returning to the Manda beds last year, he and his colleagues consulted Google Earth. "It turns out we had been walking past a big outcrop, maybe 30 metres off the path, but we could not see it through the tall grass," he says. When they got ›

back to the site, they found that the outcrop was packed with fossils.

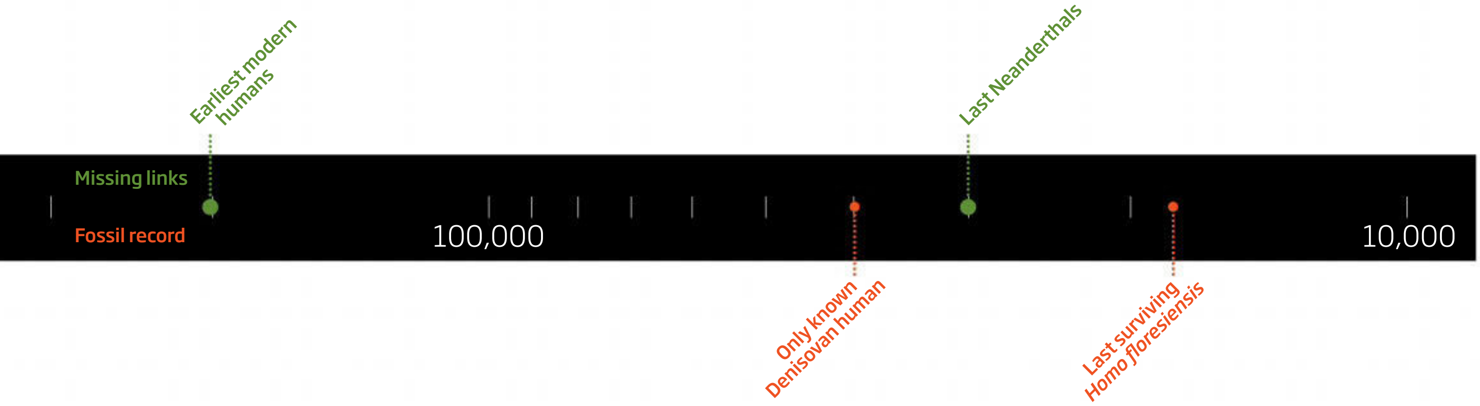
Despite these successes, one group of archosaur descendants remains elusive. Pterosaurs evolved in the early or mid Triassic, but they had hollow bones, and their ancestors were probably small and lightly built, so fossils are rare. "Nobody really knows where pterosaurs came from," says Stephen Brusatte of the University of Edinburgh, UK. "We are missing a pterosaur archaeopteryx." (See "Ancient poster child", page 56)

Like amphibians and archosaurs, modern mammals evolved following a mass extinction: the asteroid impact 66 million years ago thought to have killed off the dinosaurs. But the mammals that emerged in the subsequent 10 million years "are still an enigma", says Thomas Williamson of the New Mexico Museum of Natural History and Science in Albuquerque. Recent digs have turned up some links to modern groups, including ankle bones that show the oldest known primate, *Purgatorius*, was climbing trees 65 million years ago in what is now Montana. But other connections remain tenuous, and the oldest fossils of groups such as bats and whales do not appear until much later. Williamson and Brusatte are using techniques similar to those employed in the hunt for early archosaurs to try to understand how mammals appeared and diversified.

Meanwhile, the hunt continues at a handful of fossil beds where early mammals are preserved with soft tissue intact. In 2009, *Darwinius*, a 47-million-year-old fossil, was found in the Messel pit site near Darmstadt, Germany. Nicknamed Ida, it made a big splash as a possible missing link in the lineage leading to humans. We now know it was on a side branch that went extinct, but *Darwinius* nonetheless gives important insight into the anatomy of early primates.

We're still trying to find out how *H. floresiensis* fits into our family tree

DADEROT/NATURMUSEUM SENCKENBERG/WIKIMEDIA, CC0 1.0



As genetics has helped disentangle the origins of the earliest life forms, so it has cast light on the mysteries of our own evolution. For example, we now know that the split between the human and chimp line happened far earlier than was once thought. Using mutation rates as a molecular clock reveals that our common ancestor lived between 7 and 13 million years ago. This finding was backed up by a 2015 study of an ape that lived 12.5 million years ago, indicating that the human lineage split from chimps about 10 million years ago. Besides pointing the fossil hunters to deposits of the right age, the discovery may lead to a reassessment of ape fossils that had been deemed too ancient to be relevant.

The biggest achievement of genomics in palaeontology, however, has been to give meaning to fossil scraps. By themselves, the isolated partial finger bone, tooth and toe bone found in the Denisova cave in Siberia told us little more than that hominins had lived there about 40,000 years ago. But sequencing the DNA revealed that these unremarkable bones came from a previously unrecognised human lineage that shared ice-age Eurasia with Neanderthals and modern humans. The discovery goes far beyond finding a lost cousin: about 5 per cent of Denisovan genes survive today in the people of Papua New Guinea. Similarly, analysis of Neanderthal DNA suggests that many of us have a dash of Neanderthal ancestry.

Of course, some discoveries are still made using old-fashioned exploration. A decade ago, the world was stunned by *Homo floresiensis*, the "hobbit". Its skeletons were found on the Indonesian island of Flores, where it lived until at least 17,000 years ago. Then in 2012 came the revelation that another group of primitive humans, the Red Deer Cave people, appear to have lived in what is now China until even more recently. If researchers could find a way to extract DNA from their remains, our understanding of human evolution would be hugely enhanced. And last year a new species of human, *Homo naledi*, was identified from skeletons found by cavers exploring a South African cave.

We are better equipped than ever to solve evolution's outstanding mysteries. High-tech tools aside, today's palaeontologists also have one key advantage over their predecessors: knowledge accumulated over generations. In the field, what might once have been discarded now has a much better chance of being recognised. Nesbitt, for instance, identified an unassuming 10-centimetre-long bone as the femur of an archosaur, leading to the discovery of an entire skeleton of *Xilousuchus*, an early crocodilian.

"Almost every day there's something new and exciting, a new fossil find or publication," says Brusatte. "It is a golden age." ■

Turned to stone

Jeff Hecht and Michael Le Page pick out seven of the most amazing fossils ever discovered

Fossils can be amazing in many ways. There are unbelievable creatures like *Atopodentatus*, a marine reptile with a second row of teeth splitting its skull where its nose ought to be. Or *Helicoprion*, the shark with a circular saw for slicing up prey. There are the fossils that transformed our view of ancient life, like *Archaeopteryx*, with its strange mix of reptilian and bird-like features.

Then there are fossils with features we never expected to be preserved. Dinosaur skin imprints. Beetles whose iridescent shells still shimmer with rainbow colours. Ancient fish in whose petrified eyes the light-detecting rod and cone cells can be seen under a microscope. Yet other fossils capture our imaginations because they are so mysterious, like the enigmatic embryo-like things from 600 million years ago that don't match anything we know.

But for us, the most amazing give us a very rare glimpse not just of what animals existed, but what they were doing – fossils that transport us back in time to long-lost worlds.

THE FIGHTING DINOSAURS

Discovered: Gobi desert, Mongolia, 1971
Age: 74 million years
Location: Mongolian Dinosaur Museum, Ulan Bator

They will remain forever locked in mortal combat. The *Velociraptor* has sunk its deadly foot claw deep into the neck of the herbivore, a boar-sized creature called *Protoceratops*. This vicious attack may have hit the carotid artery – a lethal blow.

But the *Protoceratops* fought back. It has thrown the *Velociraptor* to the ground before it, and its jaws are locked on to the predator's right arm. The bite appears to have broken the *Velociraptor*'s arm. "There is no doubt these animals were fighting," says Mark Norell of the American Museum of Natural History in New York, who studied the fossil while it was on loan to the museum. "There is nothing else like the fighting dinosaurs, which captures direct evidence of a single instant in time."

What happened next? One possibility is that a sand dune collapsed on them while they were still fighting for their lives. Norell thinks heavy rains had destabilised the dune, so it flowed quickly and smoothly over the pair as they fought. Elsewhere in Mongolia, he says, animals have been found trapped in their burrows by similar flows.

Or perhaps the plant-eater bled to death from the blow to its carotid artery, trapping the injured *Velociraptor* under its heavy body.

DAVID CLARK/DINOSAURS ALIVE" IMAX FILM/GIANT SCREEN FILMS

When the predator eventually died, too, a sandstorm covered both bodies, suggests Ken Carpenter of the Utah State University Eastern Prehistoric Museum.

He points out that the *Protoceratops* is missing both forelimbs, the left hind limb and the end of its tail. This is hard to explain if they were buried alive, but could mean that scavengers found the pair dead or mortally wounded. The tight S curve of the *Velociraptor*'s neck also suggests it died before it was buried, Carpenter says. Various combinations of the two scenarios are feasible too – perhaps scavengers dug down to snatch the missing parts after the two were buried alive.

What really matters, though, is that the pair were preserved at all. Deadly duels between dinosaurs must have been an everyday event. The formidable weaponry of many meat-eaters suggests they were active predators rather than mere scavengers, but there is very little direct evidence of this. A tooth fragment found embedded in a healed tail wound, for instance, is the best evidence that *T. rex* hunted live prey.

"It looks like a freeze-frame from a dinosaur drama-documentary"

So to find two dinosaurs locked in combat, in what looks like a freeze-frame from a dinosaur drama-documentary, is absolutely extraordinary. "It's one of the best discoveries ever," says Carpenter.

"It's just so ridiculously amazing," agrees palaeontologist David Hone of Queen Mary University of London. It is surprising that a *Velociraptor* seems to have attacked an animal as big as the *Protoceratops*, he says, as most predators only tackle prey smaller than themselves.

The movie *Jurassic Park* made the name *Velociraptor* famous, but the terrifying predators in the film more closely resemble a much larger species called *Deinonychus*. *Velociraptor* was in fact quite small: 2 metres long thanks to its tail but just half a metre tall. There is no evidence these feathered fiends made up for their small size by hunting packed in hunts either. The *Protoceratops* was also about 2 metres from nose to tail tip, but much more heavily built. "The *Protoceratops* was three, four, five times the weight of the *Velociraptor*," says Hone.

Is it still the only example of its kind, though? A fossil found in 2006 in the Hell Creek formation of Montana contains bones from a tyrannosaur-like predator and a *Triceratops*-like plant eater. It was dubbed the "duelling dinosaurs" by its private owners and put up for auction for $7 million in 2013, but did not sell.

Yet the Hell Creek rocks were deposited in flowing water, so Norell thinks it more likely that the two dinosaurs were washed together by a flood than that they fought to the death. For now, then, the Mongolian fighting dinosaurs remain unique. ›

BIG MAMA
Discovered: Gobi desert, Mongolia, 1994
Age: 83 to 66 million years
Location: Mongolian Dinosaur Museum

The first oviraptor was discovered in Mongolia in 1922. It was found near a nest of what appeared to be *Protoceratops* eggs – hence its name, which means "egg thief".

In 1993, however, Mark Norell of the American Museum of Natural History found a fossilised embryo in an identical egg. He recognised it as a kind of oviraptor, suggesting the original thief was in fact a parent.

The following year, Norell was back in Mongolia when he spotted bones and claws protruding from the sand. But Norell had limited space in his trucks. The bulky fossil might have stayed where it was had team member Luis Chiappe not injured his foot. He wanted to collect a specimen rather than walk around searching for more.

A day or two later, Chiappe drove up to Norell and another team member, Jim Clark. "We found something you won't believe," Chiappe told them.

The skull of the dinosaur was missing. But much of the rest of the skeleton was present – and under it there was a nest of eggs. "It's clear it was sitting on the nest," says Clark, now at George Washington University in Washington DC. What's more, it was sitting in exactly the same position birds adopt when incubating their eggs.

There had been hints before that some dinosaurs brooded their eggs, but the discovery of Big Mama was conclusive proof. She was probably buried alive when a sand dune collapsed after heavy rains.

MICK ELLISON/AMERICAN MUSEUM OF NATURAL HISTORY

The top part of Big Mama is missing, but it's clear she was brooding her eggs

1. *The fighting dinosaurs*
2. *Big Mama*
3. *Snake eating baby dino*
4. *The mating turtles*
5. *Ichthyosaur giving birth*
6. *Fish catching fish-catching pterosaur*
7. *The Paluxy trackways*

SNAKE EATING BABY DINO

Discovered: Gujarat, India, 1986
Age: 68 million years
Location: Geological Survey of India

Unlike some dinosaurs, the giant, long-necked sauropods did not care for their eggs. Adults have never been found near nests, so it seems that sauropod hatchlings had to fend for themselves from the start. And that left the way clear for predators to feast on them as they emerged.

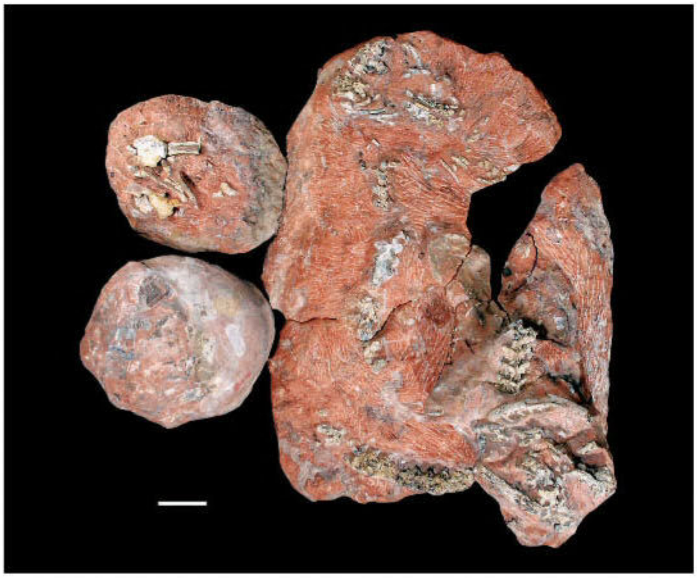
One of these predators was a 3.5-metre-long snake called *Sanajeh indicus*. Towards the end of the age of the dinosaurs, one decided to raid a nest of a sauropod eggs, perhaps attracted by the noise of hatchlings breaking out of their shells.

Sanajeh could not open its mouth wide like modern egg-eaters and other snakes, says Jeffrey Wilson of the University of Michigan at Ann Arbor, who helped describe the fossil. The eggs were 14 centimetres wide, so the snake could not swallow them whole nor break the shells, which were more than 2 millimetres thick.

Instead, the snake coiled itself around the eggs and waited for a meal to emerge. But just as it was about to gorge on a half-metre-long hatchling, a landslip buried the nest, snake and all.

The nest was originally found by Dhananjay Mohabey of the Geological Society of India in 1986. Another palaeontologist, Sohan Lal Jain, spotted a few snake vertebrae but his observation was not followed up. In 2001, Wilson also noticed the vertebrae when Mohabey showed him the fossil. He arranged for it to be taken to the University of Michigan, where much more of the snake was uncovered.

SCULPTURE: TYLER KEILLOR PHOTO: XIMENA ERICKSON



2010 WILSON ET AL.

2012 THE ROYAL SOCIETY

THE MATING TURTLES

Discovered: Messel Fossil Pit, Germany, 1987
Age: 47 million years
Location: Senckenberg Natural History Museum, Frankfurt

The French famously call it the little death. But for this pair of mating turtles, the little death became a big death. As they sank down into the depths of a lake in their post-coital bliss, they reached toxic waters and perished. Their fossil remains leave no doubt that they died in the act of mating.

Around 30 fossils of mating insects have been found, most of them caught in amber. But the turtles, *Allaeochelys crassesculpta*, are the first ancient vertebrates to be caught in the act. They lived in a volcanic lake in what is now Messel, Germany. The deep water was both anoxic and toxic, creating a death trap.

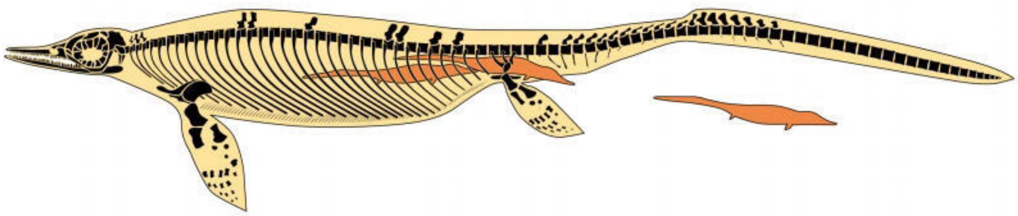
> *"The turtles are the first ancient vertebrates to be fossilised in the act"*

Allaeochelys belonged to a group of turtles with skins porous enough to absorb oxygen from water. That made them especially vulnerable to the toxins and the lack of oxygen, says Walter Joyce of the University of Fribourg in Switzerland. The turtles are particularly common in the Messel fossil pit, with 51 collected over the past few decades, including 12 pairs.

Joyce thinks at least nine of the pairs were mating. So perhaps alone among vertebrates, the *Allaeochelys* turtles in this lake had a tendency to be fossilised in the act.

No prizes for guessing what this pair were up to ›

RYOSUKE MOTANI



ICHTHYOSAUR GIVING BIRTH

Discovered: South Majiashan, China, 2011
Age: 248 million years
Location: Anhui Geological Museum, Hefei, China

Birth is a dangerous process, and for this very ancient ichthyosaur mother it went terribly wrong. She was carrying at least three offspring. One was found under the mother's body. The third was still inside her, waiting to be born. And the second was halfway out of the birth canal, making this fossil unique.

Only part of the mother was found because the team that collected the rock in 2011 had no idea it contained ichthyosaurs – they were after a predatory fish. The ichthyosaurs came to light only when the fossil was being prepared in the lab the following year. By then it was too late to recover the rest of the mother, says team member Ryosuke Motani of the University of California at Davis. But they found other fossils of the same species, *Chaohusaurus*, which were around a metre long.

There is another fossil of an ichthyosaur that might also have been giving birth. But in this case the embryo is almost entirely outside the body, and some think that it was expelled by gases as the mother, a *Stenopterygius*, decomposed on the seabed. Motani thinks this scenario is unlikely for the *Chaohusaurus*, since it had given birth to one offspring and the second was on its way out.

2012 FREY, TISCHLINGER

FISH CATCHING FISH-CATCHING PTEROSAUR

Discovered: Solnhofen, Germany, 2009
Age: 155 million years
Location: Wyoming Dinosaur Center, Thermopolis

The pterosaur flew just above the water of the tropical lagoon. Snap! It snatched a small, herring-like fish from the water and began to swallow it. But the noise attracted a predator. Up popped *Aspidorhynchus*, a sleek fish about 60 centimetres long. It leapt out of the water and grabbed the pterosaur by its left wing as it was flying. All three animals then splashed down into the water.

But the *Aspidorhynchus* had bitten off more than it could chew. It didn't have wide jaws and cutting teeth capable of dealing with such large prey. Its jaws were narrow, ending in a pointed snout, and were lined with lots of small, sharp teeth best suited to catching other fish. These teeth became entangled with the tough fibres, or aktinofibrils, that reinforced the wing membranes of the pterosaur, *Rhamphorhynchus muensteri*.

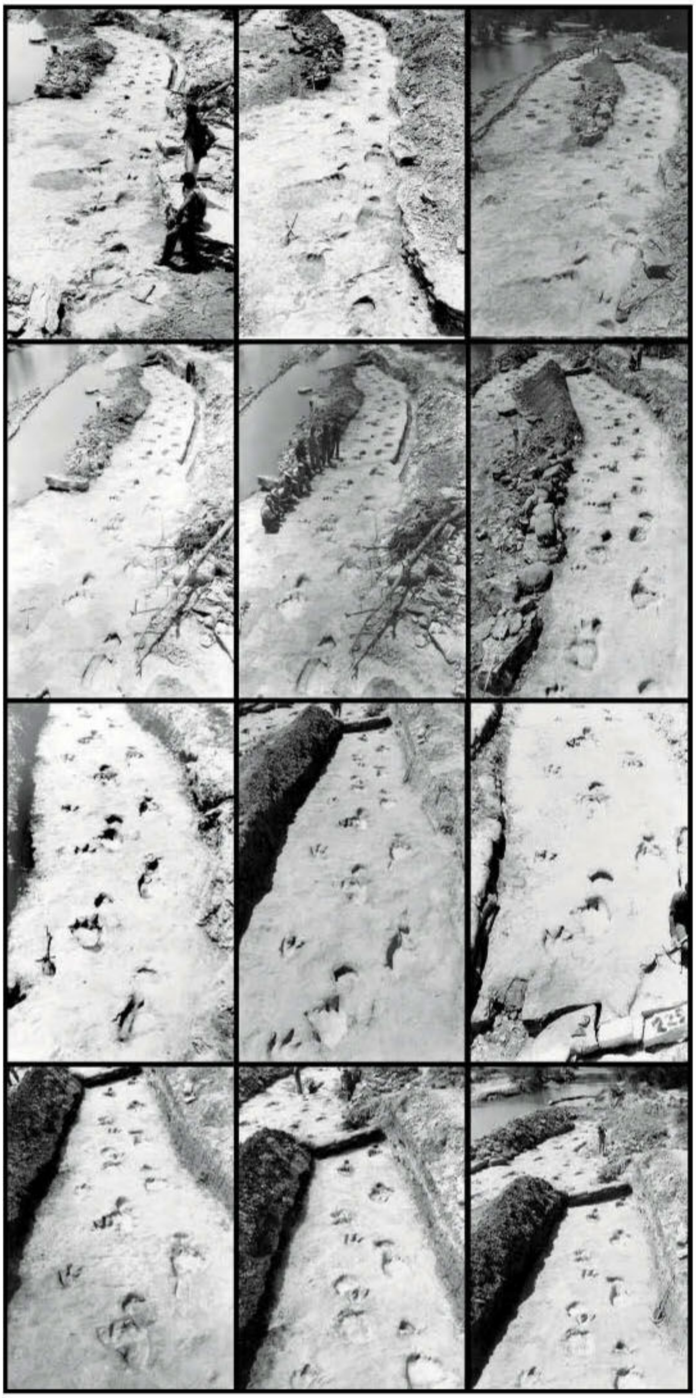
As the fish tried to shake itself free, it damaged the bones of the wing. During the struggle the pterosaur drowned, with the small

Two predators, two prey, but only three animals

fish it had caught halfway down its throat. The *Aspidorhynchus* continued its futile struggle to disentangle itself, but sank into deeper water low in oxygen and died. The bodies of all three animals ended up on the bottom of the lagoon and there they remained, beautifully preserved, until they were dug up 150 million years later.

This is the scenario proposed in 2012 by Eberhard Frey of the Karlsruhe State Museum of Natural History in Germany, who studied the fossil. We cannot be sure about all the details, but there's no doubt that the pterosaur had just caught a fish, only to be caught by a fish itself. "The attack was a lethal error on the side of *Aspidorhynchus*," Frey says. He has proposed that the pterosaur was skim-feeding – flying along with its lower beak in the water – before it was caught.

But Mark Witton at the University of Portsmouth, UK, author of the book *Pterosaurs*, says no pterosaur had any of the specialisations of skim-feeding birds, such as a reinforced skull to withstand high-speed impacts. It is more likely they flew low and dipped their jaws into the water to grab prey.



2014 FALKINGHAM ET AL

Thrill of the chase: are these the tracks of a predator and its giant sauropod prey?

THE PALUXY TRACKWAYS

Discovered: Glen Rose, Texas, 1938
Age: 111 million years
Location: Part at the American Museum of Natural History

The massive sauropod fled along the shore closely pursued by a huge predator similar to *T. rex*. The trail of footprints they left behind has survived for over 100 million years.

Exactly what happened is not clear. Roland Bird of the American Museum of Natural History, who discovered the footprints in 1938, thought they showed the predator running alongside the sauropod and at one point sinking its teeth into it, missing a step as it was lifted off the ground.

Researchers are more cautious today. There is no clear evidence of such an attack, says James Farlow of Indiana University-Purdue University in Fort Wayne, who has studied the trackway. But the predator and sauropod tracks run parallel, and at one point turn together. So it seems the predator was stalking the sauropod, not just heading the same way.

> *"It seems as if the predator was at least stalking the massive sauropod"*

There is a whole series of such tracks along the Paluxy river in Glen Rose, Texas. Many sauropods, possibly a large group, walked in one direction. Predatory theropod dinosaurs went both ways parallel to the sauropod tracks, suggesting all were walking near a shoreline.

One piece of the trackway is now on display at the American Museum of Natural History in New York. Many more remain in the Dinosaur Valley State Park along the river. ■

CHAPTER FOUR

GAIA

JUAN MANUEL CASTRO PRIETO / AGENCE VU/CAMERA PRESS

Call in the clouds

Gaia may not be so helpless after all. It seems that forests can control the weather, as **Stephen Battersby** reveals

YOU'VE done it half a dozen times today without giving it a second thought. If it was chilly in the morning, you may have turned up the heating or put on another layer. As the day got warmer perhaps you opened a window to cool things down. We are adept at controlling our immediate environment.

What about the living planet as a whole? Can the biosphere regulate the environment to suit itself, preventing the planet from freezing or boiling? This is the essence of the Gaia hypothesis proposed in the 1960s by James Lovelock, but climate scientists have never bought into it. They point out that there have been some wild swings in the climate, some of which were caused by life.

But now it appears the world would have warmed a bit more than it has were it not for the aromatic cocktail of chemicals emitted by plants. It turns out this can change the weather – and anything that changes the weather day after day and year after year changes the climate, too. While this new mechanism is nowhere near strong enough to save us from global warming, it may have been stronger in the past when the air was cleaner. So could it be that Gaia is not powerless after all?

There is no doubt that life plays many key roles in the climate system. The air we breathe, rich in oxygen with only traces of carbon dioxide, is created by plants. Trees suck up huge quantities of rainwater that would otherwise flow back into the sea, and release it into the air. Much of the rain in the Amazon may come from the trees themselves.

There are all kinds of other effects. Bacteria have been found growing in clouds, and they may help seed cloud formation. Blooms of plankton in the sea soak up the sun's heat, warming the surface. The list goes on and on.

The question is, how important are these processes? In particular, is life totally at the mercy of external influences such as the sun, or can it control the climate to some extent? Lovelock's suggestion was that living organisms work in concert with non-biological processes to regulate the environment. He pointed out that over the past 4 billion years the sun has become brighter, and yet the long-term temperature of Earth has remained suitable for life. Life might act as a planetary thermostat, Lovelock said, as well as maintaining the salinity of the oceans and other chemical balances.

To this day, Lovelock regards Gaia's existence as self-evident. "Earth's atmosphere is so massively in chemical disequilibrium, for it to stay stable for any time requires a very powerful regulating system," he says. But even if life does help control the composition of the air and seas, its ability to regulate temperature is much more dubious.

> "The chemicals that give pine forests that pleasant smell could have a huge influence on cloud formation"

We know now that there have been some violent swings in the climate, including a few "Snowball Earth" phases during which most of the planet froze, almost wiping out life. These super ice ages may well have been triggered by living organisms sucking the carbon dioxide out of the atmosphere and cooling the planet.

It is now thought Earth was saved from an icy doom by a geological thermostat. When the planet gets hot, rocks break down faster, reacting with CO_2 and removing it from the atmosphere. When it cools, this weathering process slows down, and the CO_2 emitted by volcanoes begins to accumulate in the air.

This negative feedback keeps temperatures within the "just right" Goldilocks zone, but it takes many millions of years to kick in, which still leaves room for the living part of Gaia to step up. Perhaps life usually helps prevent swings on a shorter timescale, even if things do go catastrophically wrong on occasion? What would make the idea more convincing is a clear-cut mechanism. When the temperature starts to get too high or too low, then living organisms should respond in some way to move it in the opposite direction, back towards a happy medium.

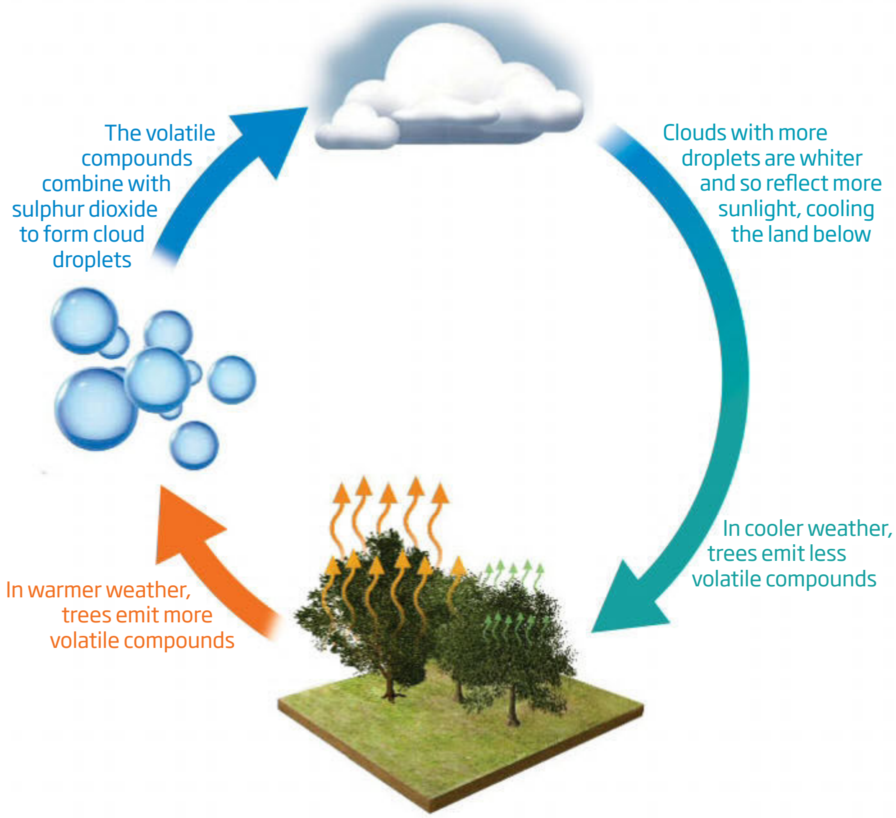
In 1987 Lovelock and others proposed one such mechanism. They pointed out that algae in the sea emit a gas called dimethyl sulphide, which can react with gases in the air to form sulphuric acid vapour and condense into small particles, or aerosols. Such aerosols can cool the planet by reflecting sunlight directly and also indirectly by making clouds whiter.

Cloud formation requires more than just cooling moist air. Water droplets do not form and grow unless the air has suitable particles, or nuclei, for the water to condense onto. These nuclei must be upwards of 100 nanometres or so in size. The sulphuric acid aerosols from dimethyl sulphide could be just the ticket if they grow large enough. When temperatures rise, the group reasoned, algae should thrive and emit more dimethyl sulphide, seeding more cloud droplets. More droplets means whiter clouds, which reflect more sunlight and cool things down, completing the negative feedback loop.

This idea, called the CLAW hypothesis ›

Climate control

How forests regulate the weather



after the initials of its four authors, inspired a lot of research – but it appears to be feeble at best. Observations show that as much as 60 per cent of the cloud condensation nuclei above the oceans are provided by salt spray, and most of the rest are solid organic compounds also sprayed directly from the sea surface. That leaves little room for the involvement of sulphate aerosols, as Patricia Quinn and Timothy Bates of the Pacific Marine Environmental Laboratory in Seattle pointed out in a 2011 review.

Another stage in the proposed feedback loop is also doubtful. "People go out on ships and incubate algae to look at their response to an increase in temperature or radiation," says Quinn. The algae do emit more dimethyl sulphide when the sea warms up, but only slightly; not enough to whitewash the sky.

So the CLAW effect seems too weak to pull Earth's climate levers. Maybe that job can be done by forests instead. In 2004 Markku Kulmala at the University of Helsinki suggested a new feedback loop. In a pine forest in southern Finland, he and his team had been measuring the concentration of a group of chemicals called terpenes. These are produced by many plants and evaporate readily into the air – they are volatile, in other words. We perceive terpenes as part of that pleasant smell of pine forests, and they are the main constituents of genuine turpentine distilled from pine resin.

As they float about in the air, terpene molecules and other volatile organic compounds become oxidised, making them less volatile. They then condense onto any tiny aerosol particles already in the air, making them larger. That means more aerosols grow to a given size. Over several years, Kulmala's group monitored terpenes and the number of aerosol particles about 3 nanometres across above a Scots pine forest in Finland. They found a strong correlation between the two, with both peaking in summer when plants are growing most vigorously. This led Kulmala to suggest that if the climate warms, plants might emit even more volatiles and make more planet-cooling aerosols – a negative feedback that would counteract the warming.

But this was only an educated guess. Kulmala's studies did not show that forests emit more volatiles as the temperature rises. Nor did it show whether the aerosol particles could grow large enough for them to seed cloud droplets – at least 100 nanometres across. And the data came from just one site – hardly evidence of a worldwide phenomenon.

Meanwhile, far from the forests of Finland, Jasper Kirkby and his team were busy making clouds in a large stainless steel chamber at the CERN particle physics laboratory near Geneva, Switzerland. In some of the experiments, the CERN team tried to recreate the first step in cloud formation: how gases condense to form embryonic aerosol particles. "If you look to the mountains one day after a rainstorm has cleansed the atmosphere, there is already a blue haze. Those are new aerosol particles that have formed from trace gases, scattering light into your eye," says Kirkby. New particles require sulphuric acid vapour to form. That comes from sulphur dioxide, a by-product of human industry as well as those marine algae.

Stick 'em together

It had been thought that sulphuric acid vapour could condense on its own, but the results of Kirkby's studies, released in 2011, proved otherwise. A few molecules might stick together, but these embryonic aerosols are unstable. They almost always evaporate instead of growing larger.

When the team added traces of ammonia to the air, however, it stabilised the growing sulphuric acid cluster, increasing the number of viable aerosol particles by as much as 1000 times. Yet this is still just a thousandth of the formation rate of sulphuric acid aerosols actually seen in our atmosphere, so something else must be stabilising their growth.

"After we ruled out ammonia, the only other possibility was organic compounds," says Kirkby. "We have now made a series of measurements with several different organics." These results came out in 2014, and showed that biogenic vapours do indeed have a major impact on the formation of aerosol particles in the atmosphere. The biological molecules not only helped the sulphate aerosols to form in the first place, they also allowed them to grow to the size of cloud-condensation nuclei, says Kirkby.

Volatile organic compounds could influence clouds in a third way, according to Gordon McFiggans's team at the University of Manchester, UK. As cloud-condensation nuclei

collect water and grow into a droplet, volatiles are absorbed along with the water, changing the chemistry of the drop to attract more water. In 2013, the team published a paper showing that this effect might substantially increase the number of droplets. And a cloud with more droplets per cubic metre is a whiter, fluffier cloud, reflecting more solar heat away from the Earth.

McFiggans is now starting experiments in Manchester to try to find out more. "We have a new photochemical chamber where we can process an atmospheric soup of gases, hit it with an arc lamp to mimic sunlight and cook up an aerosol population, then squirt it into a cloud chamber," he says. "Then we should see if we get denser clouds in the presence of organic vapours."

So several lines of evidence suggest organic compounds might have a big effect on clouds. The clincher comes from a study involving 11 weather stations around the planet. A team including Kulmala and led by Pauli Paasonen, also at Helsinki, sampled aerosols at these stations, counting the concentration of particles large enough to form a cloud droplet. They also monitored levels of a range of volatile organic compounds.

In 2013, the team reported that they had found a strong pattern. In places such as Finland and eastern Siberia, where the air is clean, the number of cloud condensation nuclei rose markedly when the temperature went up. Paasonen calculates that over these unpolluted regions, the cooling effect could be powerful, offsetting up to a third of any local temperature rise. This might be enough to protect some forested areas from the worst climate swings.

"In unpolluted regions, the cooling effect is powerful. It's as if we could cool the world by sweating"

"But in more polluted areas, the feedback is not significant," says Paasonen. That makes sense, as in these spots there is already a dense haze of aerosols. The volatiles would make those particles slightly larger but have little affect on the overall number.

Curiously, terpenes are thought to be involved in protecting individual plants from heat stress, because their release is so strongly linked to temperature. So it seems a strange coincidence that collectively they might act to cool an entire region. "It's as if we could cool the weather by sweating," says Paasonen. "That would be useful!"

Lovelock thinks it could be an evolutionary adaptation, as organisms that can regulate their climate should boost their survival. "If successful, they will spread," he says.

Globally, this cooling power of plants may not be so profound. Paasonen estimates that the feedback should offset around 1 per cent of global warming, although there is a huge uncertainty because the full effect on clouds is not well understood, and its global importance will not be clear until more sites have been studied. The true figure could be as high as 5 or 10 per cent, or much less than 1 per cent.

"It does not save us, that's for certain," says Paasonen. Nor will it be easy to indulge in a little geoengineering to boost this effect by planting certain kinds of plants, as his results suggest that the effect is just as strong over farmland as over virgin forest. But once upon a time, before human pollution overwhelmed this feedback in many parts of the world, it could have been more powerful. "One thing the authors don't go into is deep prehistory," says Tim Lenton of the University of Exeter, UK. "When land plants first evolved, this could have had a significant cooling effect."

And there may be other feedbacks working in the same direction. "When you add them up it begins to amount to something," says Lovelock. For example, volatiles may play a role at sea as well as over land, says Quinn. Salt spray is still likely to be the dominant source of cloud nuclei, but organic vapours could condense onto small salt particles to boost them to an effective size. A few teams have made observations at sea, but it is difficult to get the kind of long-term coverage that enabled Paasonen to spot the feedback on land.

So in a small way at least, Gaia can influence the temperature. Unfortunately, not only have we poisoned her and sapped her power, we have also unleashed her evil twin (see "Gaia's evil twin", page 70). As the Arctic warms, vegetation is starting to replace snow and ice, and dark vegetation soaks up more of the sun's heat – a positive feedback that is accelerating the warming in the Arctic. According to recent research, this feedback is much stronger than previously thought.

It is not clear how all this stacks up. The positive feedbacks involving living organisms may well outweigh the negative ones, undermining the notion of life making a cosy nest for itself. And even if Gaia turns out to have more power than we realised, we cannot rely on her helping hand – we still to have to save ourselves. ■

Vapourware: pollution destroys forests' ability to control the weather

FRANS LANTING/NGS.

The Earth is not a nurturing mother of life. It is far more like murderous Medea, says biologist Peter Ward

Gaia's evil twin

THE twin Viking landers that defied the odds to land on Mars in 1976 and 1977 had one primary goal: to find life. To the disappointment of nearly all concerned, the data they sent back was a sharp dash of cold water. The Martian surface was harsh and antibiotic and there was no sign of life.

To two NASA scientists, James Lovelock and Dian Hitchcock, this came as no surprise – in fact, they would have been amazed to see any evidence of life on Mars. A decade before Viking, Lovelock and Hitchcock, both atmospheric scientists, had used observations of the Martian atmosphere to deduce that there could be no life on the planet.

From their research arose one of the most influential, ground-breaking scientific ideas of the 20th century – the Gaia hypothesis, named after the ancient Greek goddess of the Earth, a nurturing "mother" of life. But is it correct? New scientific findings suggest that the nature of life on Earth is not at all like Gaia. If we were to choose a mythical mother figure to characterise the biosphere, it would more accurately be Medea, the murderous wife of Jason of the Argonauts. She was a sorceress, a princess – and a killer of her own children.

The Gaia story starts in the 1960s, when Lovelock and Hitchcock showed that the Martian atmosphere was in a state of chemical equilibrium – a stagnant pool of carbon dioxide with a dash of nitrogen but very little oxygen, methane or hydrogen. They contrasted it with our own, which they recognised as being in chemical disequilibrium, with CO_2 and oxygen levels in constant flux. The key driver of this


SARAH HOWELL

flux is life: photosynthesis exchanges CO_2 for oxygen, and aerobic metabolism does the opposite. Without life, our atmosphere would radically change from the oxygen-rich and life-sustaining gaseous mix we breathe to one in chemical equilibrium – one that, like the Martian atmosphere, would be inimical to life (see "Earth after life", page 124).

Earth's atmosphere is not only in flux, it is welcoming to life, and has been for billions of years. Similarly, Earth's surface temperature, acidity and ocean chemistry seem to have been stable for billions of years, hovering around mean values that allow continued habitability. Pondering these implications, Lovelock began piecing together a novel view of life and its interaction with the planet that hosts it. Although he focused on Earth, his ideas have implications for any habitable planet, and he has spent the rest of his career honing them.

Stated briefly, the Gaia hypothesis is that life as an aggregate interacts with the physical environment in such a way that it not only keeps the Earth habitable but continually improves the conditions for life. It does this through a series of feedback systems similar to biological homeostasis, the mechanism by which living organisms maintain a stable internal environment. Those aspects that most affect the habitability of the planet – temperature, the chemical composition of the oceans and fresh water, and the make-up of the atmosphere – are not just influenced by life, they are controlled by it.

Lovelock's concept has evolved over time, and Gaia has speciated into several different hypotheses (see "The many faces of Gaia", page 72). Within a decade of his first writings he elevated his hypothesis to the scientifically stronger Gaia theory. In the mid-1970s he described his view of things as follows: "The Gaia theory says that the temperature, oxidation state, acidity and certain aspects of the rocks and waters are kept constant, and that this homeostasis is maintained by active feedback processes operated automatically and unconsciously by the biota."

Lovelock eventually began to refer to the planet itself as some kind of superorganism. "The entire range of living matter… from whales to viruses and from oaks to algae could be regarded as constituting a single living entity capable of maintaining the Earth's atmosphere to suit its overall needs and endowed with faculties and powers far beyond those of its constituent parts," he wrote in his 1979 book *Gaia: A new look at life on Earth*. In other words, the Earth is not simply a planet that harbours life, it is itself alive. ›

The idea was simple and elegant, and quickly attracted many adherents, both scientists and non-scientists. Some researchers saw in Gaia a new way of thinking about the cycles of organic components and elements. Some followed Lovelock's lead in searching for scientific support for the idea that life regulates conditions on the planet. Some, mainly non-scientists, saw in it a new view of how humans should relate to the planet and the rest of life. Some even found the face of god in the concept.

Gaia continues to generate scientific interest and debate: there have been a number of international conferences devoted to the hypothesis. The ground is shifting, though. A number of recent discoveries have cast serious doubt on the Gaia hypotheses. Two lines of research are especially damning: one comes from deep time – the study of ancient rocks – and the other from models of the future. Both overturn key Gaian predictions and suggest that life on Earth has repeatedly endured "Medean" events – drastic drops in biodiversity and abundance driven by life itself – and will do so again in the future.

Let us turn first to the deep-time discoveries. One of the most powerful arguments made by Gaia proponents is that planetary temperatures remain steady and equable thanks to feedbacks that are caused, or at least abetted, by life.

The single most important of these various "thermostats" is the carbonate-silicate weathering cycle. Because of the constant volcanic activity that is a feature of our planet, there is an unceasing but variable input of CO_2 into the atmosphere. CO_2 is a potent greenhouse gas. Without some way of scrubbing it out, it would build up to the point where the Earth would experience runaway warming that would ultimately cause the oceans to boil away – the fate of Venus some 4 billion years ago.

That scrubbing is provided largely by chemical weathering of silicate-rich rocks such as granite. This weathering drives a chemical reaction with CO_2 that removes the gas from the atmosphere and locks it away as limestone (calcium carbonate).

The rate of this reaction is increased by land plants, whose roots break up rock and allow water and CO_2 to penetrate. Plants also directly remove CO_2 from the atmosphere through photosynthesis.

So far, so Gaian. But as scientists have made ever more precise estimates of past global temperatures, the constancy predicted by Gaia theory has been found wanting. In fact there has been a rollercoaster of temperatures, caused by the evolution of new kinds of life.

Around 2.3 billion years ago, for example, Earth endured a gigantic episode of glaciation that lasted 100 million years. It was so intense that the oceans froze completely, creating a "snowball Earth". The cause was life itself. Around 200 million years earlier, evolution had come up with a novel way to make a living: photosynthesis, the process that uses the energy in sunlight to convert inorganic CO_2 into sugars (see "The rise of the water eaters", page 28). Photosynthetic microbes sucked so much heat-trapping CO_2 out of the atmosphere that the planet was plunged into the freezer.

A second episode of snowball Earth, brought about by the evolution of the first multicellular plants, happened 700 million years ago. Much later on, the evolution of land plants gave the climate a double whammy. As well as reducing CO_2 by photosynthesis, their deep roots dramatically increased weathering rates. The result was that soon after the appearance of forests near the end of the Devonian period (416 to 360 million years ago), the Earth entered an ice age that lasted 50 million years. The warm, verdant planet cooled rapidly and vast swathes of life died out. Not a very Gaian result.

In fact, for as long as life has existed it has been well able to devastate itself. Charles Darwin envisaged newly evolved life forms entering the world like a wedge, easing into a narrow vacant niche then expanding it gradually. Some do. But others enter like a sledgehammer, smashing away entire branches of the tree of life as they arrive.

"Life seems to be pursuing its own demise, moving Earth ever closer to the day it returns to being sterile"

This has been the way since the very earliest life. Around 3.7 billion years ago, we think a "methane crisis" nearly wiped life off the face of the Earth almost as soon as it had got going. Methane-belching microbes filled the atmosphere with a hazy smog that all but blocked out the sun.

Perhaps the worst Medean event of all was precipitated by the same biological innovation that led to the first snowball Earth: the evolution of photosynthesis and the concomitant rise of atmospheric oxygen. Until that time, living things could not tolerate oxygen – it was a deadly poison to the microbes that constituted life before 2.5 billion years ago. With the evolution of photosynthesis a weapon of mass destruction was unleashed, creating the first, and perhaps the most extreme, of all mass extinctions. Life was devastated. All that survived were photosynthesisers and microbes that evolved rapidly to tolerate oxygen.

Even more damning to the Gaia hypothesis are results from the study of the mass extinctions that have occurred since the evolution of animals 565 million years ago, of which there have been five big ones and about 10 more minor ones (see "Death on a massive scale", page 114).

When in 1980 geologists made the ground-breaking discovery that the Cretaceous/Tertiary mass extinction of 65 million years ago was caused by an asteroid hitting the Earth, it soon became orthodoxy that all mass extinctions had been caused by extraterrestrial events: either impacts or, in the case of the Ordovician extinction 443 million years ago, a gamma-ray

The many faces of Gaia

There are at least three different variants of the Gaia hypothesis

OPTIMISING GAIA

This early interpretation remains one of the "strongest" versions of Gaia theory. It implies that life actively controls environmental conditions, including purely physical aspects of the biosphere such as temperature, oceanic acidity and atmospheric gas composition, such that the Earth remains optimally habitable.

SELF-REGULATING (OR HOMEOSTATIC) GAIA

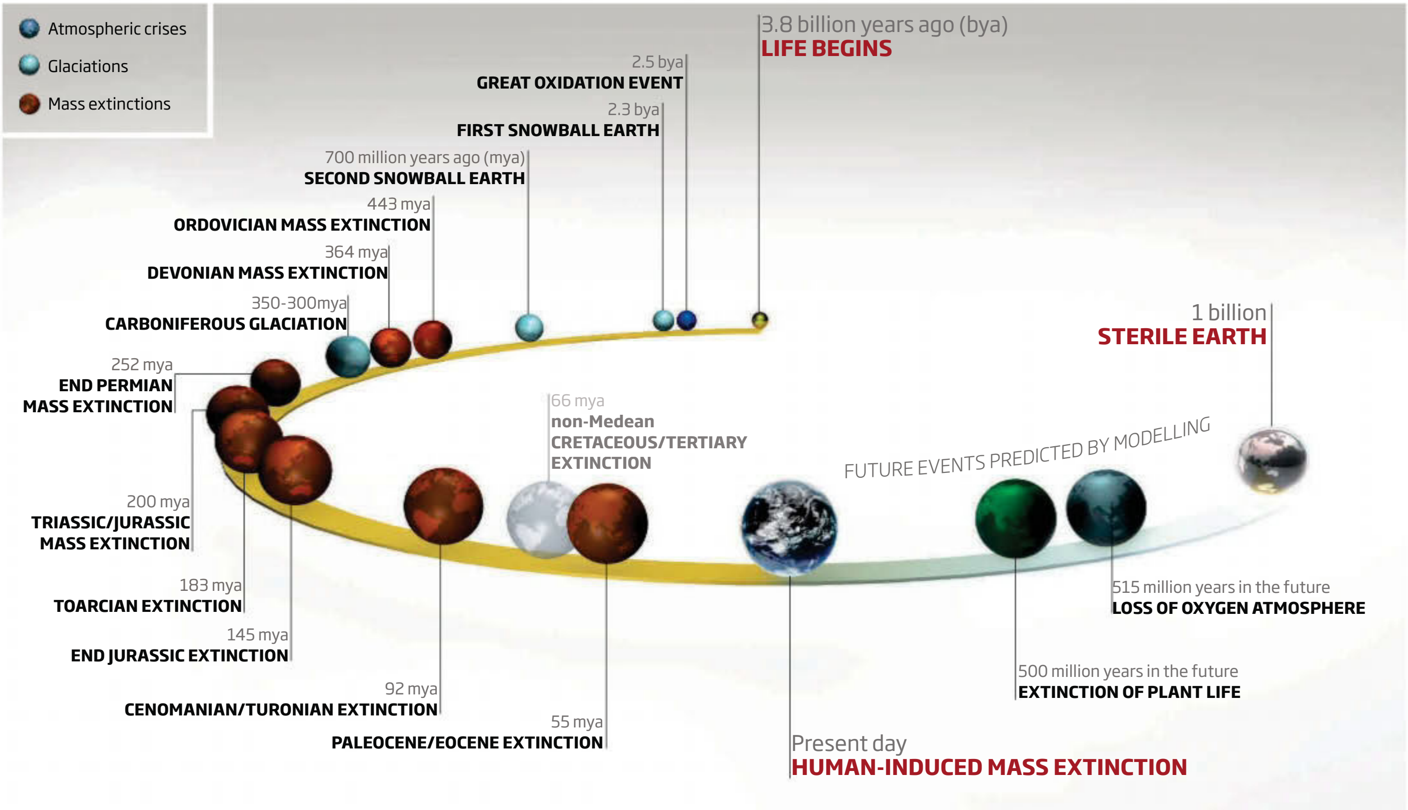
A more recent and slightly weaker incarnation of the theory. Rather than life actively optimising conditions on the planet, it creates negative feedback systems that keep life-constraining factors such as temperature, and more recently atmospheric oxygen and carbon dioxide levels, within certain ranges.

SUPERORGANISM GAIA

The Earth isn't just a physical planet that supports life, it is itself alive. This is the strongest interpretation of the theory and tends to be viewed as unscientific.

When life kills life

Almost all mass extinctions have been caused by one type of life killing another, with the notable exception of the Cretaceous/Tertiary mass extinction, which is thought to have been the result of an asteroid impact



burst. These events are termed "Gaia neutral", because life has no way of preparing for them.

Researchers quickly identified impact craters apparently associated with mass extinctions, including the huge Permian/Triassic event of 251 million years ago and the Triassic/Jurassic event 200 million years ago. Yet the evidence that impacts cause mass extinctions has not stood up to scrutiny. Most are now seen as "microbial" mass extinctions, caused by huge blooms of bacteria belching poisonous hydrogen sulphide gas. These blooms thrive in the stagnant oceans that arise during intense episodes of global warming, such as the one at the end of the Permian, when prolonged volcanic activity vented vast amounts of CO_2 into the atmosphere. According to Gaia theory, life should have buffered these events. But it did not. Far from being Gaian, their existence seems to strongly support the Medean view, as do many other events in the history of life including, arguably, the human-induced mass extinction that is going on around us now.

What of the future? Here too we can refute Gaia, and this is perhaps the most interesting – and shocking – of discoveries. Life seems to be actively pursuing its own demise, moving Earth ever closer to the inevitable day when it returns to its original state: sterile.

How so? The starting point is that the sun is getting hotter. It has increased in brightness by about 30 per cent over the past 4.5 billion years and will carry on doing so. As the sun continues to burn brighter it will cause global warming, which will translate into increased weathering of silicate rocks – the rate of weathering rises with temperature. This will remove CO_2 ever faster from the atmosphere, aided and abetted by photosynthesis and plant roots.

Calamity strikes

At first, this removal of CO_2 will buffer the solar-induced temperature increase. But there will come a time – possibly as early as 500 million years from now – when there is not enough CO_2 in the atmosphere to support photosynthesis. When that calamitous day arrives, a very pronounced end of the world as we know it will begin.

The changes will be dramatic and catastrophic to life. Plants will wither and die, shutting off the main source of biological productivity and atmospheric oxygen. Animals will quickly follow. The loss of plants will also lead to a renewed build-up of CO_2 in the atmosphere, leading to a runaway greenhouse. Eventually, the temperature of the Earth's surface will exceed that of boiling water, and the last microbe will perish. Earth will be lifeless once more. This is very anti-Gaian, since the theory states that the presence of life on a planet should extend its habitability. The opposite is true.

If these models are correct, life on Earth is already in its old age. The adventure that started 3.8 billion years ago, and is still the only life we know of in the universe, has maybe another billion years to run. The long-term, and terminal, decline of CO_2 in the atmosphere has already started – the effect of burning fossil fuels is just a blip. Gaia is dying. Long live Medea. For now. ■

Gaia: the verdict is...

James Lovelock's Gaia theory took the world by storm when it was first put forward in the 1970s. But is it right? Oceanographer **Toby Tyrell** says the knowledge we have built up in the past 40 years points to a clear answer

LIFE has steered Earth's environment over billions of years, helping to keep it stable and comfortable for living things. That's the crux of James Lovelock's Gaia hypothesis, which addresses enduring questions such as "how does our planet work?" and "how is it that Earth has remained continuously habitable for more than 2 billion years?"

Gaia is a fascinating hypothesis, but is it right? Working out the answer is particularly significant as we battle to be stewards of a planet with a human population of 7 billion and rising. If we don't understand how our planet's environment works, how can we know the best way to preserve it?

I first became interested in Lovelock's idea when I read his book *Gaia: A new look at life on Earth* and became intrigued by the idea that our planet could regulate itself. That interest influenced my career, eventually leading me to oceanography. But at the same time, I wasn't sure that things could really be as simple as Lovelock had suggested.

Lovelock made powerful arguments in favour of the Earth as a self-regulating system, but I could see no conclusive proof that the hypothesis was correct. So I began to investigate its feasibility in more detail, carrying out research into pertinent questions such as whether the ocean's nitrate levels could be regulated by a "nitrostat" – a natural stabilising mechanism analogous to a thermostat.

I was also fortunate to attend several conferences on Gaia, in Valencia, Spain, and in Oxford, along with luminaries such as the evolutionary biologists Bill Hamilton and John Maynard Smith; Lynn Margulis, who established endosymbiosis, the idea that one organism can live symbiotically within another; and Heinrich "Dick" Holland, an expert in the great oxygenation event, when oxygen first accumulated in the air. These meetings were a cross-disciplinary melting pot and led to an exciting exchange of ideas of a breadth we seldom find today.

As I did more work, I realised that although there was a wealth of literature on Gaia, no one had made a thorough investigation of the whole hypothesis. I decided to attempt one. My approach was to dissect the Gaia hypothesis into component assertions, scrutinising each in turn.

Lovelock's books and articles propose three main arguments for Gaia: (1) that Earth is an extremely favourable habitat for life; (2) that life has greatly altered the planetary environment, including the chemical composition of the atmosphere and the sea; and (3) that Earth's environment has remained fairly stable over geological time.

Climate record

I tested these assertions against the latest scientific evidence. In the decades since the Gaia hypothesis was proposed, our knowledge has grown enormously. We now have long climate records from ice cores; we have devised experiments to test the idea of kin selection – that it can make evolutionary sense for an organism to sacrifice its own reproductive success to boost that of a close relative; and we can reconstruct ice-age landscapes and vegetation. I tried to determine not only whether each assertion seemed correct in light of modern data but also whether, if correct, it constituted strong evidence in favour of the Gaia hypothesis over alternatives.

Analysis of the first claim – that Earth's environment is favourable for life – led me to look at ice ages. The environmental scientist Stephen Schneider considered these to be a strong argument against Gaia. I, too, found plenty of evidence that they are rather unfortunate times for life. During past ice ages the amount of terrestrial vegetation was reduced to about half that of warmer interglacial periods, and about three-quarters of the area now covered by shallow seas – the most productive parts of the ocean – became dry land when the sea level fell.

Climate cycles and ice ages seem incompatible with the Gaian notion of a hospitable planet

The main driver of ice ages is not life but Milankovitch cycles, the periodic variations in the way the Earth orbits the sun, which are purely a matter of physics. However, life is implicated in the low temperatures which allow ice ages to occur because life is involved in the carbon cycle, which in turn controls atmospheric carbon dioxide and

MICHAEL APPELT/ANZENBERGER/EYEVINE

Although Lovelock's second claim is clearly correct, it is not a clincher for Gaia because it could equally well support a competing idea. The "coevolution of life and planet" hypothesis posits that life and the environment influence each other but with no requirement that the outcome improve or maintain Earth's habitability. There is no compelling reason to favour Gaia over this alternative.

What about Lovelock's third claim, that the Earth's environment has remained fairly stable over geological time? This is contradicted by evidence for climate cycles punctuated by ice ages. We also have evidence of long-term variations in the concentrations of the major ions in seawater, and of snowball/slushball Earth events, when our planet may have completely frozen over. There is also the great oxygenation event itself, which caused a mass poisoning of anaerobic organisms.

I also considered other topics, such as whether there is any obvious mechanism for Gaia. The hypothesis would be instantly more plausible if it could be seen to arise naturally out of evolution. Although I found no convincing reasons to believe this, I did come across some fascinating cases of "Gaias in miniature". For instance, the interiors of termite mounds and wasps' nests are strongly thermoregulated, experiencing much smaller day-night temperature fluctuations than the air outside. These stable internal temperatures come about partly because of how these social insects orientate their nests, but also through corrective group behaviours when brood temperatures drop too low or rise too high.

These are great examples of Gaia in action, but they do not lead us to expect that something similar must happen at the global scale. It turns out that communal regulation of a shared environment has so far been observed only in closely related individuals, whereas the global biota is the opposite – genetically extremely diverse.

My research led to a clear outcome: that the Gaia hypothesis is not an accurate picture of how our world works. Unfortunately, our planet is less robustly stabilised than Gaia implies, and therefore more fragile. In some ways it is a shame that this beautiful idea doesn't hold true, but it is far better that we tackle environmental issues based on an accurate view of how our Earth system operates rather than a flawed one. ■

"On a Gaian planet, life engineers more favourable environmental conditions"

thus Earth's greenhouse warming.

Also unhelpful for life are the forms in which nitrogen is found on Earth. Vast quantities of it are present in the air and sea as inert molecules made of two nitrogen atoms, which only nitrogen-fixing microbes can make use of; much rarer are forms more easily used by life, such as nitrates. This leads to widespread nitrogen starvation despite the element's superabundance. Earth's nitrogen cycle is run almost entirely by microbes – but the outcome is the exact opposite of what ought to happen on a Gaian planet, on which life would be expected to engineer more favourable environmental conditions.

When I looked into Lovelock's second claim, I found it to be supported. There is plenty of evidence of biological alteration of the global environment. For instance, life affects the planetary albedo – the degree to which Earth reflects solar energy back out to space – through the generation by ocean microbes of dimethyl sulphide, a chemical that influences cloud formation.

However, this effect, long held up as confirming Gaia, has turned out to be relatively weak. And there's another catch.

MUTT INK

CHAPTER FIVE

EVOLUTION

The ultimate guide to a beautiful theory

If you think you understand it, you don't know nearly enough about evolution, says Michael Le Page

IT IS now 207 years since the birth of Charles Darwin and more than 150 years since the publication of *On the Origin of Species*, perhaps the most important book ever written. In it Darwin outlined an idea that many still find shocking: that all life on Earth, including us humans, evolved through natural selection.

Darwin presented compelling evidence for evolution in *On the Origin* and since his time the case has become utterly overwhelming. Countless fossil discoveries have allowed us to trace the evolution of today's organisms from earlier forms. DNA sequencing has confirmed beyond any doubt that all living creatures share a common origin. Innumerable examples of evolution in action can be seen all around us, from the famous pollution-matching pepper moth to the emergence of diseases such as AIDS and H5N1 bird flu. Evolution is as firmly established a scientific fact as the roundness of the Earth.

Yet despite the ever-growing mountain of evidence, most people around the world are not taught the truth about evolution, if they are taught about it at all. Even in the UK, the birthplace of Darwin, a 2006 poll suggests less than half the population accepts evolution.

For those who have never had the opportunity to learn much about biology or science in general, the claims about evolutionary theory made by those who believe in supernatural alternatives can appear convincing. Even among those who do accept the reality of evolution, misconceptions still abound.

Most of us are happy to admit that we do not understand, say, string theory in physics, yet we would baulk at saying the same about evolution. In fact, as biologists are discovering, evolution can be stranger than their predecessors ever imagined. So here is *New Scientist*'s guide to a few common myths and misconceptions about evolution.

1 EVERYTHING IS AN ADAPTATION

Contrary to popular belief, not all characteristics of plants and animals are adaptations or the result of natural selection

Why do so many of us spend our evenings in front of the TV with a microwave meal? Could it be that television is the modern equivalent of a Neolithic fire, making TV dinners "the natural consequence of hundreds of thousands of years of human evolution", as a researcher once concluded?

Stop laughing. It is very tempting to invent evolutionary "just so" stories to explain almost any aspect of our body or behaviour. We all tend to assume that everything has a purpose – but we are often wrong.

Take male nipples. Male mammals clearly do not need them. They have them because females do: it doesn't cost much to grow a nipple, so there has been no pressure for the sexes to evolve separate developmental pathways, to switch off nipple growth in males. Some researchers claim the female orgasm exists for the same reason, though this is far more controversial.

Or consider your sense of smell. Do you

2 EVOLUTION CAN'T BE DISPROVED

There are all sorts of findings and experiments that could have falsified evolution, but in the century-and-a-half since Darwin published his theory, not a single one has done so

When asked what would disprove evolution, the biologist J. B. S. Haldane famously growled: "Fossil rabbits in the Precambrian." What he meant was that evolution predicts a progressive change over time in the millions of fossils unearthed around the world: multicellular organisms should come after unicellular ones; jawed fish should come after jawless ones, and so on. All it would take is one or two exceptions to challenge the theory. If the first fossil amphibians were older than the first fossil fish, for example, it would show that amphibians could not have evolved from fish. No such exceptions have ever been found anywhere.

The discovery of a mammal-bird hybrid, such as a feathered rabbit, could also disprove evolution. There are animals with a mixture of mammalian and reptilian features - such as the spiny anteater - and there are fossils with a mixture of bird and reptilian features, such as the toothy archaeopteryx. But no animals have a mixture of mammalian and bird features.

This is exactly what you would expect if birds and mammals evolved from separate groups of reptiles, whereas there is no reason why a "designer" would not have mixed up these features, creating mammals with feathers and bird-like lungs, or furry, breastfeeding ostriches.

A young Earth would also be a problem for evolution, since evolution by natural selection requires vast stretches of time - "deep time" - as Darwin realised. Some thought evolution had been falsified in the 19th century when physicist William Thomson calculated that the Earth was just 30 million years old. In fact, several lines of evidence, such as lead isotopes, show the Earth is far older than even Darwin imagined - about 4.5 billion years old.

Suppose for a moment that life was designed rather than having evolved. In that case, organisms that appear similar might have very different internal workings, just as an LCD screen has a quite different mechanism to a plasma screen. The explosion of genomic research, however, has revealed that all living creatures work in essentially the same way: they store and translate information using the same genetic code, with only a few minor variations in the most primitive organisms. Huge chunks of this information are identical or differ only slightly even between species that appear very different.

What's more, the genomes of complex creatures reveal a lack of any intelligence or foresight. Your DNA consists largely of millions of defunct copies of parasitic DNA. The inescapable conclusion is that if life was designed, the designer was lazy, stupid and cruel.

Not only that, if organisms had been designed for particular roles, they might be unable to adapt to changing conditions. Instead, countless experiments, both planned and unplanned, show that organisms of all kinds evolve when their environment is altered, provided the changes are not too abrupt. In the laboratory, tweaking organisms' environments has enabled researchers to produce bacteria, plants and animals with all kinds of novel characteristics - even entirely new species. In the wild, human activity is reshaping many species: urban birds are diverging from their country cousins, some fish are getting smaller because fishermen keep only big fish, and trophy hunting is turning bighorn sheep into smallhorns, for instance.

find the scent of roses overwhelming or struggle to smell anything at all? Can you detect the distinctive odour that most people's urine acquires after eating asparagus? People vary greatly when it comes to smell, and this is probably less to do with natural selection than with chance mutations in the genes coding for the smell receptors.

Then there are features which do result from selection, but for another trait entirely. For instance, the short stature of pygmies might have no survival advantage in itself, but instead be a side effect of selection for early childbearing in populations where mortality is high. Similarly, since the same gene often has different roles at different times of development or in different parts of the body, selection for a variant that is beneficial in one way can have other, seemingly unrelated effects. Male homosexuality might be a side effect of genetic variants that boost female fertility. What's more, a mediocre or even poor gene variant can spread rapidly through a population if it happens to be located near a highly beneficial gene.

Other features of plants and animals, such as the wings of ostriches, are adaptations no longer needed for their original purpose. These vestigial traits can persist because they make no difference to an individual's chances of survival, or they have taken on another function, or because even though they have become disadvantageous, they occur in a population that is too small or has undergone too few generations for evolution to eliminate them.

A prime example in humans is the appendix. While claims abound that it has this or that function, the evidence is clear: you are more likely to survive without an appendix than with one. Another example is wisdom teeth. Having a smaller, weaker jaw allowed our ancestors to grow larger brains, but left less room for molars. Yet many of us still grow teeth for which there is no room, and the consequences can be fatal.

Evolutionary psychology in particular is notorious for attempting to explain every aspect of human behaviour, from gardening to rape, as an adaptation that arose when our ancestors lived on the African savannah. Some behaviours may indeed be past adaptations, but in the absence of any proof, claims about TV dinners should be taken with a large pinch of salt.

"Why are there no feathered mammals or furry, breastfeeding ostriches?"

DAVE WATTS/NATUREPL.COM

3 EVOLUTION IS LIMITLESSLY CREATIVE

It might seem as though there is no end to nature's inventiveness, but there are probably some features that could never evolve, at least on Earth

It often seems that nature invented pretty much everything that can be invented long before humans arrived on the scene, even a form of wheel. There is a salamander living in the Californian mountains that coils itself up and rolls downhill when threatened. The pearl moth caterpillar goes one better and can roll itself along a flat surface for four or five revolutions to escape predators.

Even so, there are structures that would clearly be useful but have never evolved: lions would steer clear of zebras with built-in machine guns, for example. Why can evolution invent some things but not others?

It's a very tricky question. One way to answer it is to start with a question used by deniers of evolution to suggest that many of nature's inventions – the eye, the bacterial flagellum – are too complex to have evolved. What use is half a wing, they ask?

Very useful, is the answer. The wings of insects might have evolved from flapping gills that came to be used for rowing on the surface of water. This is an example of exaptation – structures and behaviours that evolved for one purpose taking on wholly new functions, while remaining useful at every intermediate stage.

Turn this argument around, however, and it does suggest that some features cannot evolve because half of them really would be no good. For example, two-way radio would be useful for animals – for making silent alarm calls, perhaps, or tracking down their companions – so why hasn't it evolved? The recent invention of nanoscale radio receivers suggests it is not physically impossible.

The answer might be that half a radio really is useless. Detecting natural radio waves – from lightning, for instance – doesn't tell animals anything useful about their environment. That means there will be no selection for mutations that allow organisms to detect radio waves. Equally, without any means of detecting radio waves, emitting them serves no useful purpose either.

The contrast with visible light could hardly be greater. Simply detecting the presence or absence of light is a big advantage in many environments, a very blurry picture is better than no resolution at all, and so on.

Emitting visible light can be helpful too, even for creatures that cannot detect it themselves. For the bioluminescent phytoplankton that light up ocean waves, for instance, it is a way of summoning predators that eat the phytoplankton's own enemies. A similar argument applies to sound: it is not hard to see how forms of echolocation evolved independently in groups such as bats, cave swiftlets and whales.

Another impossibility seems to be plants that float in the sky like balloons. The idea doesn't seem too far-fetched at first glance: many seaweeds have floats called pneumatocysts, filled with oxygen or carbon dioxide. Other algae can produce hydrogen. Fill a large, thin pneumatocyst with hydrogen and perhaps a seaweed could fly. Flying plants would beat water and land plants to the light, so why aren't our skies green?

The trouble is that there is no pressure for large pneumatocysts with thin membranes to evolve, as these would be more vulnerable to predators and wave damage. What's more, algae produce hydrogen only when there's a lack of sulphur, and hydrogen would leak out of any pneumatocyst. Half a hydrogen balloon doesn't look very good for anything. Evolution almost certainly has its limits.

4 NATURAL SELECTION LEADS TO EVER GREATER COMPLEXITY

Actually natural selection can lead to ever greater simplicity, and complexity may initially arise when selection is weak or absent

Use it or lose it. That old adage applies to evolution as well as everyday life, and explains why cave fish are eyeless and parasitic tapeworms gutless.

Until recently, such examples were considered the exception, but it seems we may have seriously underestimated the extent to which evolution likes to simplify matters. There are entire groups of apparently primitive creatures that are turning out to be the descendants of more complex organisms. For instance, the ancestor of brainless starfish and sea urchins had a brain; why their descendants dispensed with a brain is still unclear.

Despite this, there is no doubt that evolution has produced ever more complex life forms over the past four billion years. This is usually assumed to be the result of natural selection, but recently some biologists studying our bizarre and bloated genomes have turned this idea on its head. They propose that, initially at least, complexity arises when selection pressure is weak or absent. How could this be?

Suppose an animal has a gene with two different functions. As a result of mutation some offspring may get two copies of this gene. In a large population where competition is fierce and selection pressure strong, such mutations are likely to be eliminated because they do not increase an individual's fitness and are probably slightly disadvantageous.

In smaller populations where selection pressure is weak, however, these mutations have a small chance of surviving and spreading as a result of random genetic drift (see page 87). If this happens, the duplicate genes will start to acquire mutations of their own. A mutation in one copy might destroy its ability to carry out the first of the original gene's two functions, while the other copy might lose the ability to perform the second function. Again these changes don't confer any advantage - such animals would still look and behave exactly the same - but these mutations might also spread by genetic drift. So the population would have gone from having one gene with two functions to two genes with one function each.

This increase in genomic complexity would have occurred not because of selection pressure but despite it. Yet it can be the foundation of greater physical or behavioural complexity because each gene can now evolve independently. For example, either can be switched on or off at different times or in different tissues. And as soon as any beneficial mutations arise, natural selection will kick in.

It seems there are opposing pressures at the heart of evolution: while complex structures and behaviours, such as eyes and language, are undoubtedly the product of natural selection, strong selection - as in large populations - blocks the random genomic changes that can throw up greater complexity in the first place.

POLKA DOT/JUPITER

5 EVOLUTION PRODUCES PERFECTION

You don't have to be perfectly adapted to survive, you just have to be as well adapted as your competitors are. The apparent perfection of animals is more a reflection of the poverty of our imaginations than of reality

It's a theme endlessly repeated in wildlife documentaries. Again and again we are told how perfectly animals are adapted to their environment. It is, however, seldom true.

Take the red squirrel, which appeared to be perfectly adapted to its environment until the grey squirrel turned up in the UK and demonstrated that it is in fact rather better adapted to broadleaf forests.

There are many reasons why evolution does not produce perfect "designs". Natural selection only requires something to work, not to work as well as it could. Botched jobs are common. The classic example is the panda's "thumb", a modified wrist bone that the animal uses like an opposable thumb to grasp bamboo. It's far from the ideal tool for the job, but since the panda's true thumb is fused into its paw, the panda had to settle for a clumsier alternative.

Evolution is far more likely to reshape existing structures than throw up novel ones. The lobed fins of early fish have turned into structures as diverse as wings, hoofs and hands. What this means is that we have five fingers because amphibians had five digits, not because five fingers is necessarily the optimal number for the human hand.

Many groups haven't evolved features that would make them better adapted. Sharks lack the gas bladder that allows bony fish to precisely control their buoyancy, and instead have to rely on swimming, buoyant fatty livers and, occasionally, gulping air. Mammals' two-way lungs are far less efficient than those of birds, in which the air flows in one direction.

Continual mutation also means that potentially useful features can get lost. Many primates cannot make vitamin C, an ability that wasn't missed in animals that get lots of vitamin C in their diet. However, such losses can be limiting if the environment changes, as one primate discovered on long sea voyages.

Evolution's lack of foresight also leads to inherently flawed designs. The vertebrate eye, with its blind spot where the wiring goes through the retina, is one example. Once natural selection fixes upon a bad – but workable – design, a species' descendants are usually stuck with it.

Environments also change. In the arms race between predator and prey, parasite and host, species have to keep evolving just to maintain their current level of fitness, let alone get even fitter. As the Red Queen says in *Through the Looking Glass*: "It takes all the running you can do, to keep in the same place."

Humans aren't running fast enough. Evolving and adapting is a numbers game: the larger a population and the more generations there are, the more mutations will appear and the more chances there will be for natural selection to favour the beneficial and eliminate the harmful. Around 10 billion new viral particles can be produced every day in the body of a person infected with HIV; the total human population on Earth was no more than a few million until fairly recently. A bacterium can produce 100,000 generations in a decade, but there have probably been fewer than 25,000 generations since the human lineage split from that of chimpanzees. So it's hardly surprising that in less than a human lifespan, we've seen the evolution of new viruses, such as HIV.

Our evolution has accelerated in the last 10,000 years, but we are changing our environment ever faster, leading to problems ranging from obesity and allergies to addictions and short-sightedness. Viruses and bacteria might approach perfection: we humans are at best a very rough first draft.

AMOS NACHOUM/CORBIS

6 IT DOESN'T MATTER IF PEOPLE DON'T GRASP EVOLUTION

At an individual level, it might not matter very much. However, any modern society which bases major decisions on superstition rather than reality is heading for disaster

So your brother or mother is a creationist. Let them believe what they want, you might think. After all, that makes family get-togethers a lot easier and it make no difference to anyone else.

Or does it? If a Republican wins the 2016 US election the world's biggest superpower will be run by a man who rejects evolution, thanks to the support of the tens of millions of people in the US who also cannot accept reality. It is dangerous when leaders prefer dogma to biological reality: Stalin's support for the pseudoscience of Trofim Lysenko was a disaster for Soviet agriculture.

The success of western civilisation is based on science and technology, on understanding and manipulating the world. Its continued success depends on it, perhaps now more than ever as sources of cheap, easily available energy start to dry up and climate change kicks in. Any leader who thinks evolution is a matter of belief is arguably unfit for office. How can a leader capable of ignoring the staggering amount of evidence for evolution assembled by researchers in myriad fields possibly judge the more subtle scientific evidence for, say, climate change?

What's more, evolution is directly relevant to many policy decisions. Infectious diseases from tuberculosis to wheat rust are making a comeback as they evolve resistance to our defences. Antibiotic-resistant superbugs like MRSA are a growing problem. A deadly virus such as H5N1 bird flu or Ebola might evolve the ability to spread from human to human at any time, leading to a devastating pandemic. It is not possible to grasp how serious the threat is and plan for it unless you understand the power of evolution.

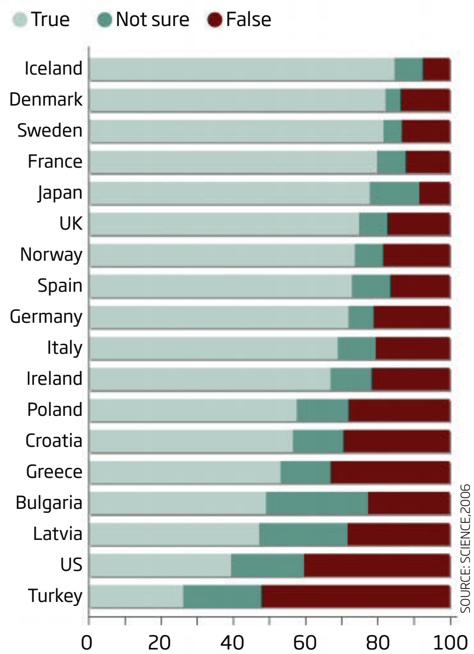
There are many more subtle areas where understanding evolution matters too. For instance, fishing policies that allow fishermen to keep only large fish are leading to the evolution of smaller fish. The tremendous changes we are making to the environment are altering many species, from rats becoming resistant to poisons to urban birds that are changing their songs to counter noise pollution (see "Unnatural selection", page 112).

There is our future, too. Modern biology is on the brink of giving us previously unimaginable power over the human body, from reshaping embryos to rewriting the genetic code to delaying the effects of ageing. Societies' views on if and how these powers should be used will inevitably be shaped by people's understanding of their evolutionary origins. Things look rather different depending whether you think we are a perfect, finished product or a crude early prototype thrown up by a desperately cruel process from whose clutches we now have the opportunity to start to free ourselves.

This is not to say that evolutionary theory tells us how to run societies or make ethical decisions. It doesn't. It is a descriptive science, not a prescriptive one. It does, however, help us to make informed decisions.

Acceptance of reality

Adults were asked about this statement: "Human beings, as we know them, developed from earlier species of animals"



7

EVOLUTIONARY SCIENCE IS NOT PREDICTIVE

We cannot say exactly what life will look like in a billion years, but evolutionary theory can make a few predictions

Cosmologists make precise predictions about what will happen to the universe in 20 billion years time. Biologists struggle to predict how a few bacteria in a dish might evolve over 20 hours. Some claim that this lack of precise predictive power means evolution is not scientific.

However, what matters in science is not how much you can predict on the basis of a theory or how precise those predictions are, but whether you can make predictions that turn out to be right. Meteorologists don't reject chaos theory because it tells them it is impossible to predict the weather 100 per cent accurately – on the contrary, they accept it because weather follows the broad patterns predicted by chaos theory.

The difficulty in predicting the path of evolution partly springs from organisms' freedom to evolve in quite different directions. If we could wind the clock back 4 billion years and let life evolve all over again, its course might well be different. Life on this planet has also been shaped by chance events. If an asteroid had not wiped out the dinosaurs, intelligent life might have been very different, if it evolved at all.

Nevertheless, although evolution's predictive power might appear limited, the theory can and is used to make all sorts of predictions. For a start, Darwin predicted that transitional fossils would be discovered, and millions – trillions if you count microfossils – have been uncovered. What's more, researchers have predicted in which kinds of rocks and from what eras certain transitional fossils should turn up in, then gone out and found them, as with the half-fish, half-amphibian *Tiktaalik*.

Or take the famous peppered moth, which evolved black colouring to adapt to pollution-stained trees when industrialisation took place. Remove the pollution and, evolutionary theory predicts, the light strain should once again predominate – which is just what is happening.

This predictive power can also be put to much more practical use. For instance, evolutionary theory predicts that if you genetically engineer crops to produce a pesticide, this will lead to the evolution of insect strains which resist that pesticide, but it also predicts that you can slow the spread of resistance genes by growing regular plants alongside the GM ones. That has proved to be the case. Many researchers developing treatments for infectious diseases try to predict how resistance might evolve and to find ways to prevent this from happening, such as prescribing certain drugs in combination. This slows the evolution of resistance because pathogens have to acquire several different mutations to survive the treatment.

BRISTOL CITY MUSEUM/NATUREPL.COM

8 NATURAL SELECTION IS THE ONLY MEANS OF EVOLUTION

Much change is due to random genetic drift rather than positive selection. It could be called the survival of the luckiest

Take a look in the mirror. The face you see is rather different from that of a Neanderthal. Why? The answer could be genetic drift. With features such as the shape of your skull, which can vary in form with little change in function, chance might play a bigger role in evolution than natural selection.

DNA is under constant attack from chemicals and radiation, and errors are made when it is copied. As a result, each human embryo contains 100 or more new mutations. Natural selection will eliminate the most harmful – those that kill the embryo, for instance. Most mutations make no difference because they occur in junk DNA, which makes up the vast majority of our genome. A few cause minor changes that are neither particularly harmful nor beneficial.

While most new neutral mutations die out, a few spread through later generations purely by chance. The odds of this happening are tiny, but the sheer number of mutations that arise make genetic drift a significant force. The smaller a population, the more powerful it is.

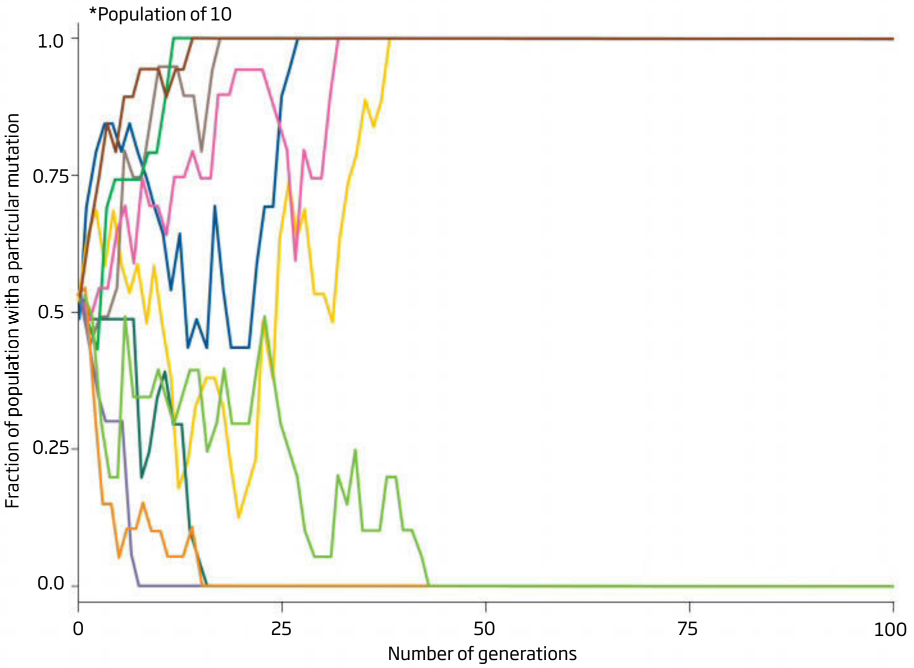
Population bottlenecks have the same effect. Imagine an island where most mice are plain but a few have stripes. If a volcanic eruption wipes out all the plain mice, striped mice will repopulate the island. It's survival of the luckiest, not the fittest.

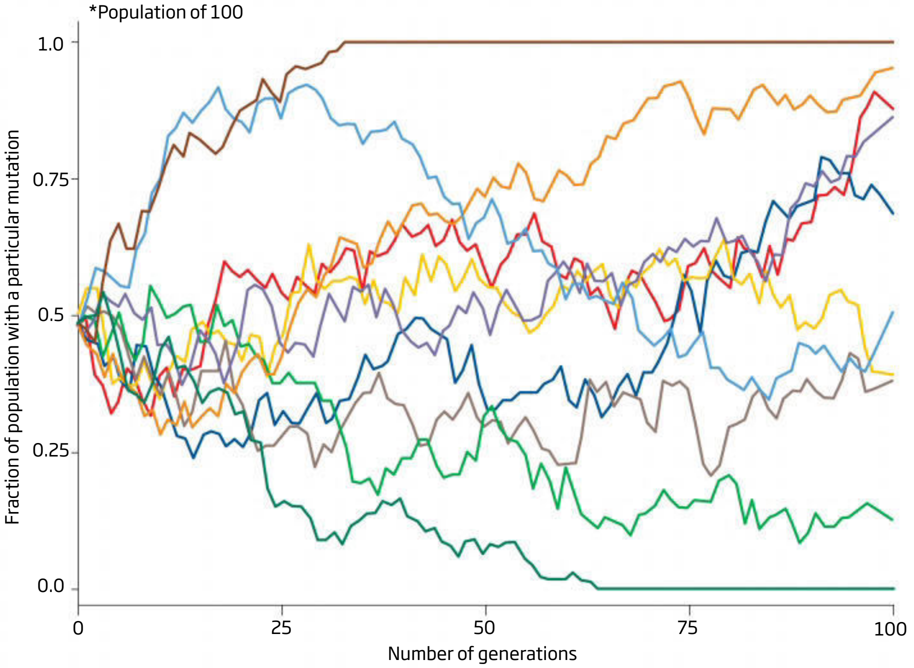
These processes have almost certainly played a big role in human evolution. Human populations were tiny until around 10,000 years ago, and genetic evidence suggests that we went through a major bottleneck around 2 million years ago.

Most of the genetic differences between humans and other apes – and between different human populations – are due to genetic drift rather than selection, but as most of these mutations are in the nine-tenths of our genome that is junk, they do not make any difference. Of those that do affect our bodies or behaviour, it is likely that at least a few have spread because of drift rather than selection. ■

Genetic drift

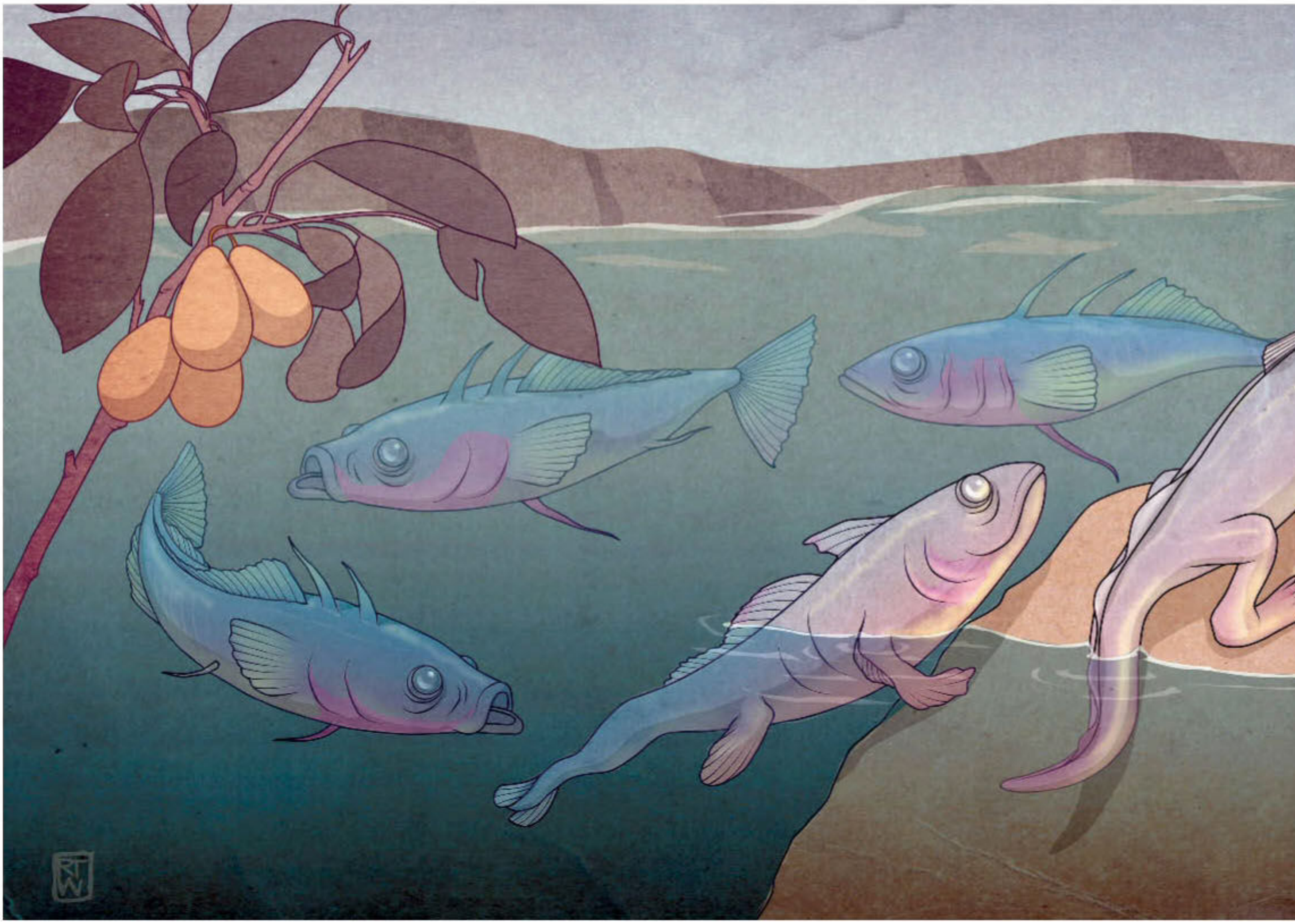
Natural selection is not the only force in evolution. Mutations that have little or no effect on fitness can spread throughout a population or die out due to chance alone. Each graph shows 10 simulation runs from the same starting point





*A population of diploid individuals, meaning each can have 0, 1 or 2 copies of any mutation

SOURCE: UNIVERSITY OF CONNECTICUT



RICHARD WILKINSON

In the fast lane

Evolution is usually portrayed as slow and steady, but that couldn't be further from the truth. Michael Le Page reports

MICHAEL BELL has his children to thank for his discovery. Back in 1990, they were getting restless as he was driving past Loberg Lake in Alaska. Bell, a biologist who studies the evolution of sticklebacks, had not planned to collect any fish, as the native sticklebacks had been exterminated in 1982 to improve the lake for anglers. "But we saw the lake, and we had to do something," Bell says.

To Bell's surprise, they found that marine sticklebacks had recolonised the lake. This in itself was not all that unusual: marine sticklebacks can live in fresh water, and most freshwater species are descended from marine ones that colonised streams and lakes as the ice retreated at the end of the last ice age.

But there was something odd about these sticklebacks. Ten thousand years on from the ice age, freshwater sticklebacks are quite different from their sea-going ancestors. The most obvious change is loss of armour plates, which seem to take longer to develop in fresh water. In lakes, lightly armoured fish may outgrow and outcompete fully armoured fish.

This trait was assumed to evolve slowly, over thousands of years, so Bell was surprised to find that some of the fish he caught in

Loberg Lake had fewer plates. In 1991 he asked a friend to collect some more fish. Sure enough, more had lost their armour.

Bell, who is based at Stony Brook University in New York, began collecting sticklebacks every year. Each time, he found more lightly armoured fish. By 2007, 90 per cent were of the low-armour form. Far from taking millennia, the trait had evolved in a couple of decades (see diagram, page 88).

Compared with the gradual process described by Darwin, this is evolution at warp speed. What is really startling, though, is that far from than being exceptional, high-speed evolution is starting to look like the norm. Very few biologists set out to look for evidence of ongoing evolution, but wherever they do, they find it – from weeds and pests to fish to humans (see "We are evolving too", page 90). It now appears that whenever the environment changes in any way, life evolves. Fast.

Such findings throw up a paradox. The two main ways to study evolution – the fossil record and comparisons of genomes of living organisms – suggest that the process is gradual, with some species barely changing over tens of millions of years. If evolution is as rapid as some biologists now claim, how come the fossil record and genetic studies suggest it is usually very slow?

Reports of rapid evolution go back a surprisingly long way. It turns out that British entomologist Albert Farn wrote to Darwin in 1878 to point out that darkly coloured annulet moths were becoming more common than lighter moths in areas blackened by pollution. This was nearly 20 years before it was first suggested that the famous peppered moths were turning black for the same reasons.

"Wherever people look for rapid evolution, it's there. Very fast change can occur in very short periods"

In 1897, it emerged that several insect populations were becoming resistant to insecticides. By the 1930s, more examples had surfaced, such as scale insects developing resistance to hydrogen cyanide.

Over the following decades, biologists stumbled upon more and more examples. A few became famous, such as the peppered moth, but all were regarded as curiosities. "People went, 'wow, that's amazing, that must be the exception'," says Michael Kinnison of the University of Maine in Orono, one of the first researchers to set out specifically to look at evolution in action.

Today, there are probably thousands of examples, and a growing number of biologists think that far from being an exception, rapid evolution is common. "Wherever people look for it, it's there," says Kinnison. "Very fast change can occur in very short periods." And thanks to advances in genetics, we are beginning to understand how it is possible.

Bell's stickleback record remains one of the best-documented examples. Besides losing armour, the fish have also acquired other traits typical of freshwater fish, such as smaller gills. Their immune systems have also evolved to cope with different threats. Research from earlier this year even shows that a population of stickleback fish in Lake Constance, Switzerland, is splitting into two species before our eyes. The one living the main lake has longer spines and tougher ›

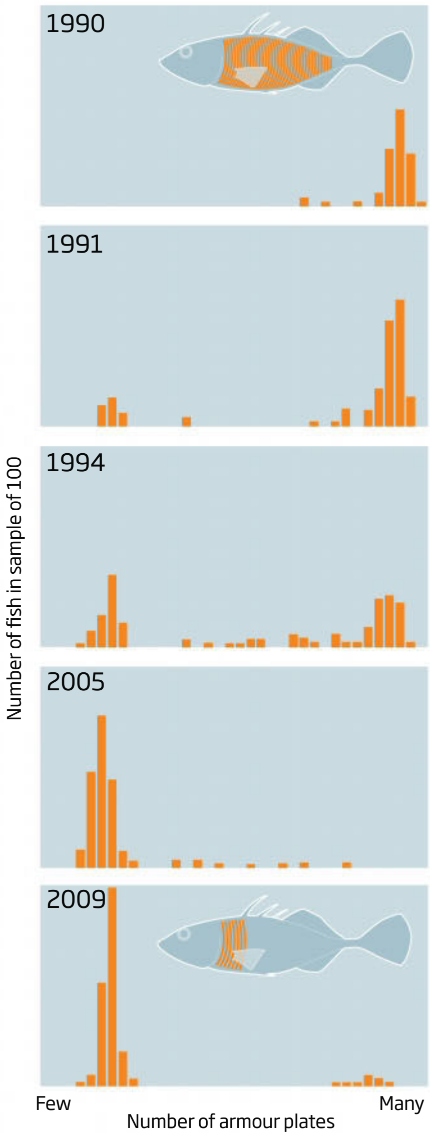
armour compared with the other, which lives in the streams flowing into the lake.

From genetic studies we know that armour loss is due to mutations in a gene called *EDA*, which plays a role in skin development. These mutations are also found in marine sticklebacks, although they are very rare. They persist at low levels because the trait is recessive, meaning fish lose their armour only if they inherit two mutant copies of the gene.

But once the sticklebacks move into fresh water where less armour is an advantage, the mutations are desirable and rapidly become more common as natural selection does its work. This explains how the same trait evolved repeatedly as sticklebacks colonised lakes after the ice age.

Ready, steady, evolve!

Freshwater sticklebacks are known to evolve from heavily armoured marine forms. Samples from Loberg Lake in Alaska show that it can happen in less than 20 years



SOURCE: MICHAEL BELL, STONY BROOK UNIVERSITY

Such pre-existing genetic diversity seems to be what allows populations to evolve rapidly. Support for this idea comes from a study of sticklebacks in Cook Inlet, Alaska, which recently switched to living in fresh water. The armour of these fish has hardly changed at all, and Bell's team has found that they are less genetically diverse than those in Lake Loberg.

While rapid evolution usually involves existing mutations, new ones can play a role too. For instance, the mosquito *Culex pipiens* evolved resistance to organophosphate insecticides when an unusual mutation produced several copies of one gene, enabling it to make more of an enzyme that could break the pesticides down. This new mutation has spread worldwide.

In the right circumstances, even new species can evolve in next to no time. In 1866, farmers in the US reported that an unknown maggot was attacking their apples, a crop introduced two centuries earlier. Entomologist Benjamin Walsh suggested that the "apple maggot" was a strain of the native hawthorn fly that had switched diets. Walsh had previously suggested this kind of process could lead to speciation.

We now know that Walsh was right. Genetic studies have shown that the hawthorn fly appears to be in the process of splitting into two species. What's more, the parasitic wasps whose larvae feed on the maggots are also splitting into two species.

More examples keep turning up. A species of fish in a lake in Nicaragua has split in two in only 100 years. The new variety has evolved a narrower, pointier head and fatter lips, ideal for nibbling insects from crevices. The original variety has sturdier jaws and extra teeth to crack snail shells. Lab studies suggest the strains do not mate with each other even when put together, which would mean they are on their way to becoming separate species.

Yet another example comes from the famous Galapagos finches. Since 1973, husband-and-wife team Peter Grant and Rosemary Grant have been studying the finches on the island of Daphne Major, in one of the few long-term studies of ongoing evolution. Their work was made famous in *The Beak of the Finch* by Jonathan Weiner.

They reported in 2010 that a new species of finch might be evolving. In 1981, a medium ground finch (*Geospiza fortis*) from another island reached Daphne Major and interbred with the local birds, producing offspring with unusual beaks and songs. After four generations, following a severe drought that killed many birds, this new strain stopped interbreeding with the other finches. It's not clear why interbreeding stopped, but if the birds continue to shun the locals they will become a new species.

As the list of examples grew, Kinnison and his colleagues began to pull them together and look at what they tell us about evolution. "We started to realise that maybe this was not the exception, that this was the norm."

In fact, he now argues that the term "rapid evolution" is misleading, because it implies evolution is normally slow. Instead, he and his colleagues prefer "contemporary evolution".

Nowadays, most biologists with a background in evolution appreciate this, Kinnison thinks. Of course, proving that contemporary evolution is the norm in a world of millions of species is a challenge. To those who remain sceptical, though,

"We started to realise that maybe rapid evolution was not the exception, it was the norm"

RICHARD WILKINSON

EVOLVE TO AVOID THE HEAT

If species can evolve very rapidly (see main story), does that offer them a way to cope with sudden environmental change? It's an intriguing possibility, but as yet nobody really knows. "Some animals will be able to change fast enough, but others will not," says Michael Kinnison of the University of Maine in Orono.

For example, most bird and mammal species have already suffered a huge loss of genetic diversity as a result of human pressures, so they are not well placed to evolve in the face of dramatic climate change.

According to Ary Hoffmann of the University of Melbourne and Carla Sgrò of Monash University in Clayton, both in Australia, rapid evolution is likely to help some species survive but we don't yet have enough information to identify the winners and losers, nor to take evolution into account in programmes designed to reduce biodiversity loss.

Kinnison's response is simple: "Take a look."

If rapid evolution really is the norm, how come fossil and genetic studies suggest it is slow? The answer may be that new species and traits not only evolve rapidly, they also disappear fast too and do not leave their mark on the fossil or genetic record.

The best example also comes from the Galapagos. In 1977 a drought on Daphne Major wiped out plants that produce small seeds, and many of the ground finches that fed on them died. Those with larger beaks that enabled them to feed on bigger seeds did better, and within a few generations beak size had increased by around 4 per cent. The wet year of 1983 saw small seeds become abundant again and soon beak size had shrunk again – evolution had gone into reverse.

Speciation can also go into reverse. On the nearby island of Santa Cruz, two incipient species are collapsing back into one. Work in the 1960s showed the finches on this island had split into large and small-beaked strains, specialising in different-sized seeds. Now most have medium-sized beaks, probably as a result of people feeding birds rice, making small or large beaks less of an advantage.

Many other examples are being discovered. Lake Victoria in east Africa is home to more than 500 species of cichlid fish, many of which split off in the past 15,000 years. Now many species are merging back together.

The reason is that females recognise males of the same species by their bright colours. As the lake has become murkier due to human activity, females are increasingly breeding with the wrong males, giving rise to hybrids that eventually replace the two original species.

This evolutionary toing and froing may well be the norm. As a result of fluctuating selection pressures, populations probably evolve rapidly in one direction and then the other, ending up back where they started.

Evolutionary yo-yoing can also be driven by the interactions between species, not just external factors like the weather. Around a decade ago, Nelson Hairston's team at Cornell University in New York began experimenting on single-celled algae and tiny animals called rotifers that feed on them. They expected to see a classic predator-prey cycle – a decline in algae as rotifers increased, followed by a rotifer crash as they ran out of food, leading the algae to rebound, and so on.

In fact, they saw unexpected patterns. Sometimes rotifer numbers grew even when algal numbers remained constant. The reason, Hairston realised, was that these algae were evolving rapidly, alternating between putting resources into defence or into multiplying – which creates more rotifer food. Rotifer numbers sometimes increased at just the right rate to keep the rapidly reproducing algae in check. When the team repeated the experiments with genetically identical algal cells, to slow evolution to a crawl, they saw classic cycles.

Hairston later discovered that theoretical biologists had predicted that rapid ›

Galapagos finches are still inspiring discoveries into the processes of evolution

AP PHOTO/SCIENCE, B. ROSEMARY GRANT

evolution could produce the kinds of patterns he saw. What remains unclear is how common it is in the wild. "It must happen sometimes, but how often? That's the $64,000 question," says Hairston.

One place this kind of cycle might be getting under way is the Hawaiian island of Kauai, where the crickets recently fell silent. In the 1990s, a parasitic fly arrived which tracks down male crickets calling for mates and deposits its egg on them. The larvae then devour the crickets alive. The cricket population plummeted.

In 2003, the island was still silent – so Marlene Zuk of the University of Minnesota was surprised to find plenty of crickets there. It turned out that almost the entire population had a mutation that alters the wings of male crickets and prevents them making any sound when rubbed together. The population has survived because a few males can still chirp. Silent males gather around these males and intercept potential mates.

For Zuk, the interesting question is what will happen next. At present, the crickets are heading down an evolutionary dead end. "I don't think that a completely silent population could survive," says Zuk. Instead, she suggests, we will see a predator-prey cycle driven by rapid evolution, similar to the ones Hairston observed. As silent males increase, parasite numbers may fall, leading to a rebound in singing males followed by a parasite revival, and so on.

Switching direction

There is nothing new about the idea of an evolutionary arms race in which species have to continually evolve to keep up – it is called the Red Queen hypothesis. What is new, though, is the idea that not only can this kind of evolution occur far more rapidly than once thought, but that the runners in the race keep switching direction.

This has important practical implications. If you want to model pest outbreaks or the spread of parasitic diseases, say Hairston, you have to take evolution into account. "If you leave that out, you are going to get the answer wrong." As a result, the study of how contemporary evolution affects population dynamics has rapidly become a hot topic.

Put it all together and the picture of evolution that is emerging is radically different to the way most people envisage the process. As Kinnison puts it, the popular view of evolution is upside down. People think evolutionary changes are imperceptible in the short term but add up to big changes over millions of years. In fact, the opposite is true. It now appears that organisms evolve very rapidly in response to any changes in their environment, but in the longer term most evolutionary changes cancel each other out.

So the longer the period you look at, the slower evolution appears – a phenomenon first pointed out in 1983 by Philip Gingerich of the University of Michigan, Ann Arbor. At the time nobody believed it, but "people have recognised now that it was a very insightful piece of work," says Hairston.

"I think a superficial reading of the fossil record has given us a misleading picture of the evolutionary process," says Gingerich. "The changes seen over long intervals of geological time are not representative of what happens on a generation-to-generation timescale."

This is especially true of long periods with little or no evolutionary change. The conventional explanation for this stasis has been that evolution is usually slow because selection is usually weak. "But this is perfectly consistent with strong selection, providing it fluctuates," says Graham Bell of McGill University in Montreal, Canada.

Assuming it is right, this new picture of evolution should perhaps come as no surprise. We have always known that the "march of progress" is an illusion, that evolution is a random process with no purpose. Rather than going somewhere slowly, evolution usually goes nowhere fast. ■

WE ARE EVOLVING TOO

Love takes many forms. Members of the Fore tribe of Papua New Guinea used to believe that when someone died, their loved ones should eat every bit of the body. The daughters ate the brain and sometimes fed titbits to their children.

This tradition led to the spread of a degenerative brain disease called kuru. Like Creutzfeldt-Jakob disease, it is caused by a rogue prion protein that accumulates in the brain. Kuru killed nearly all the young women in some villages. But a few did not succumb. They were the descendants of a person born around 200 years ago with an unusual mutation in the prion protein that stops it going rogue. As kuru became widespread, the mutation rapidly became more common. Half of the women in the areas most affected now carry the mutation, which has not been found anywhere else in the world. If the tradition of cannibalism had not been stopped in the 1950s, it would have become even more common among the Fore.

The emergence of kuru resistance is one of the clearest examples of very rapid human evolution but it is far from the only one. Around 3000 years ago, the ancestors of Tibetans split from the population that gave rise to the Han people of China. As soon as they began living at altitude, the population began to adapt. While some of the adaptations are a result of living in the mountains - a bit like altitude training in athletes - some are genetic.

One variant in a gene controlling the production of red blood cells, for instance, is found in 78 per cent of Tibetans but just 9 per cent of Han people. And the process has not stopped. "We think the selection process is ongoing," says Rasmus Nielsen of the University of California, Berkeley, who led the study.

More evidence comes from a study of Tibetan women living above 4000 metres. Those with high levels of oxygen in the blood had 3.6 surviving children on average, whereas those with low oxygen levels had just 1.6, due to much higher infant mortality. That suggests the genetic variant thought to be responsible for higher blood oxygen levels is being passed on in greater numbers and becoming more common.

STUART KOLAKOVIC

The X factor

A single gene could illuminate Darwin's greatest mystery. **Bob Holmes** reports

ALTHOUGH Charles Darwin titled his book *On the Origin of Species*, speciation was one thing he could not explain. He called it the "mystery of mysteries", and even a century-and-a-half later the mechanism by which two groups of animals become genetically incompatible remains one of the greatest puzzles in biology. We understand how Darwin's Galapagos finches could have evolved from a single species – different populations became isolated and gradually adapted to different environments until they were no longer able to reproduce with each other. However, speciation also occurs rapidly and without physical isolation of populations, which is far harder to explain. Yet, amazingly, a single gene could hold the key.

That gene is at the heart of a crucial but seemingly irrelevant process called genetic recombination. During the production of eggs and sperm, chromosomes pair up, cross over and swap segments of DNA, mixing the genes you inherited from your mother and father (see diagram, page 94). This shuffling of the genetic pack is the source our individual uniqueness. But no one suspected that recombination might also play a role in generating new species.

The breakthrough came with the discovery that the gene that controls genetic exchange, which goes by the prosaic name of *PR-domain containing 9*, or *Prdm9*, is also implicated in generating reproductive incompatibility between different members of the same species. Dubbed "the speciation gene", if *Prdm9*'s two roles turn out to be linked, it could be evolution's missing X factor.

The story of *Prdm9* begins in 1974 with a young geneticist named Jiri Forejt at what was then the Czechoslovak Academy of Sciences in Prague. He was cross-breeding two subspecies of mouse, when he discovered that male offspring of certain combinations of parents were unable to reproduce. Further crosses indicated that differences in an unidentified gene were at least partly responsible for this reproductive isolation. In effect, the gene was creating two species. It was the first speciation gene known in vertebrates, and the first one known to cause "hybrid sterility". At that stage, though, its identity remained elusive.

Fast forward to the turn of the millennium, when Forejt and his colleagues finally cornered their culprit – a gene called *Prdm9*.

Meanwhile, at the University of Oxford, evolutionary biologist Chris Ponting had begun what seemed like a totally unrelated research project: rummaging through the human genome in search of the genes that make us unique. "If you want to know what makes humans human, you need to find out which gene has evolved fastest in humans," Ponting says. To his surprise, he came up with the same gene Forejt had tagged just a few months earlier – *Prdm9*. "It has the claim of being the most rapidly evolving gene in human history," says Ponting. Humans and chimps differ at more than 7 per cent of the DNA letters in *Prdm9*, which is over five times the average difference between the species.

Why, Ponting wondered, should his search for an evolutionary sprinter turn up a so-called speciation gene, rather than one affecting some uniquely human trait such as language or a large brain? When he

"Variation in this gene could be driving a wedge between different parts of our human population"

looked more widely, the answer became apparent: *Prdm9* evolves with extraordinary rapidity throughout the animal kingdom, from rodents and sea anemones to snails and worms. It is not special to humans at all.

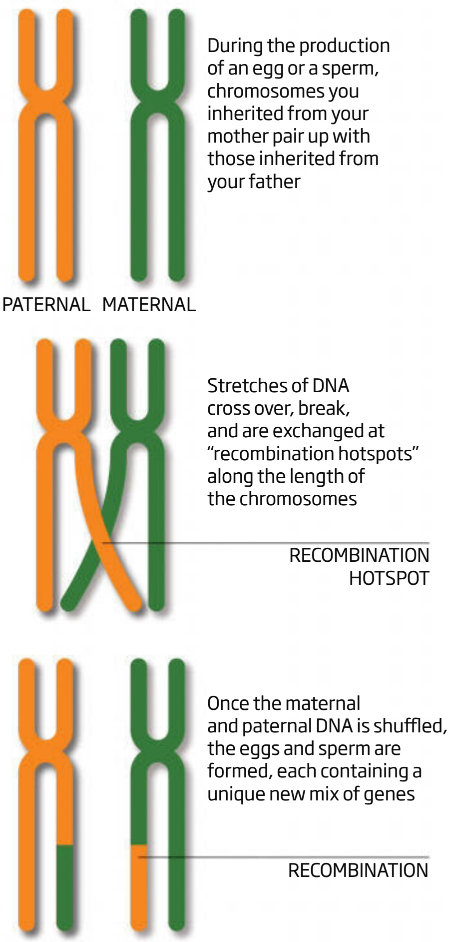
Ponting's search for human uniqueness had hit a dead end. But Forejt's esoteric mouse gene was starting to look more and more interesting. Here was a gene with a clear evolutionary role, yet also linked to sterility, an evolutionary dead end. The key to resolving the contradiction surely lay in finding out *Prdm9*'s function. "No gene evolves to make sterile mice," says Michael Nachman, an evolutionary geneticist at the University of California, Berkeley. "*Prdm9*'s role in hybrid sterility is an accidental by-product of its proper role." But what was that role? The answer soon came, from yet another direction.

Genetic recombination was first described a century ago, but research had not moved on much since 1931 when geneticist and Nobel laureate Barbara McClintock demonstrated the mechanism of crossing over. However, the ability to sequence entire genomes sparked renewed interest in recombination, particularly in the question of where exactly crossover occurs. It had been assumed that it happens randomly across the genome, but closer inspection revealed that at least 80 per cent of crossover events happen at so-called "hotspots" of recombination. (There are at least 25,000 in the human genome, although when an egg or sperm is produced only a tiny fraction of these is active.) This arrangement makes sense, if hotspots exist to channel crossovers away from crucial parts of the genome. "Recombination involves breaking DNA, and when you mend DNA you sometimes make mistakes," says Gil McVean, a statistical geneticist at the University of Oxford. So sticking hotspots near but not in genes could certainly be seen as a good thing."

Then, in 2008, McVean and his colleague Simon Myers discovered that about 40 per cent of hotspots have the same 13-letter DNA sequence, or motif. They realised that something probably homes in on that motif to activate the hotspot and trigger recombination. The most likely candidate for the job would be a so-called zinc-finger protein – a key-like molecule that recognises and binds to particular DNA sequences, usually to initiate the process of transcription.

In 2010, three research groups independently identified the protein involved. It was indeed a zinc-finger protein. And the gene responsible for making it? You guessed it – our friend *Prdm9*. We now know that Prdm9 binds to all locations that become recombination hotspots, and the 13-letter sequence is one of set of related motifs.

Last-minute mix-up



The discovery of *Prdm9*'s function can at least shed light on why it evolves so rapidly. Each time a crossover occurs, part of the DNA sequence around the break is lost, erasing the hotspot motif on the chromosome to which the Prdm9 protein is bound. The cell patches this hole by copying the sequence from the undamaged region of the other chromosome of the pair. But occasionally an individual carries the hotspot motif at that location on only one chromosome, and the repair erases the hotspot. So as eggs and sperm are produced, and time goes on, hotspots should gradually wink out, one by one, until none remain. Obviously, that does not happen, and *Prdm9* provides the reason: while mutations in most genes tend to be damaging, any mutation that changes the Prdm9 protein's zinc fingers will simply alter the sequence of DNA to which it binds, gradually creating new hotspot motifs. "You need recombination, so you don't want to be eroding motifs," says McVean. "But if you've got a gene that is constantly changing what it binds to, erosion won't be a problem. You'll be moving motifs before it has caught up with you."

Moreover, *Prdm9* is built for change. The protein it codes for has several zinc fingers – 12 or 13 in most human versions – whose coding sequences line up one after the other in a structure called a minisatellite. These are unusually prone to mutation, so *Prdm9* seems well equipped to hold up its end of the evolutionary race against eroding hotspots. In fact, the zinc fingers of the Prdm9 protein can bind to motifs within the *Prdm9* gene itself, making it a recombination hotspot in its own right, according to work led by Alec Jeffreys, the inventor of DNA fingerprinting, at the University of Leicester, UK. This makes it even more prone to rapid evolution.

All this paints a very busy picture of the genome. In a time-lapse sequence running over hundreds or thousands of generations, hotspots would constantly be blinking on and off throughout the genome, with *Prdm9* as the engine driving this incessant drumbeat of change. At the very least, this means that individuals who carry different variants of the *Prdm9* gene will differ in the hotspots they use, and perhaps even in the recombination strategies they employ (see "Ways to shuffle a genome", above right). McVean notes that this could also affect the sorts of genetic diseases to which different people are prone, since errors

in recombination resulting in accidental duplication or deletion of DNA often cause specific diseases such as Charcot-Marie-Tooth disease and certain hereditary neuropathies.

What's the link?

So *Prdm9*'s role in recombination can explain its very rapid evolution, but what about the link with speciation? Does specifying the points at which chromosomes swap material somehow give *Prdm9* the power to make certain combinations of egg and sperm incompatible, or are these two, independent abilities combined in one gene by sheer coincidence? Most *Prdm9* researchers lean towards the first explanation. "It makes sense that there must be some common mechanism," says Forejt.

Mice with incompatible variants of *Prdm9* are clearly sterile, and the link between recombination and fertility is becoming clearer – at least in mice. Using a mouse model, Forejt's group recently showed that hotspot asymmetry seems to be the driver of hybrid infertility. Unexpectedly, this infertility could be reversed by replacing the mouse sequence with the human one. Other new research on hotspots in birds and yeast, which both lack *Prdm9* and have stable recombination hotspots among related species, shows that speciation and hotspot evolution are not necessarily tightly coupled, McVean says.

But what about humans? We know that different lineages of humans sometimes carry different variants of *Prdm9*. In most Europeans, for example, the Prdm9 protein has 13 zinc fingers, but the number ranges from eight to 18. In Forejt's mice, differences like that can be enough to produce sterile offspring. Might the same be true of humans? Ponting thinks it is worth investigating. "Variation in this gene could be driving a wedge between different parts of our human population," he says.

It is an intriguing idea, but the evidence to date seems not to corroborate it. Jeffreys and colleagues compared the sperm count of men who had inherited the same version of *Prdm9* from each parent with that of men who had inherited different versions. The "hybrid" men showed no tendency to lower sperm counts, as estimated by DNA yield from sperm samples.

Of course sperm count is not the only measure of fertility, and may be irrelevant in understanding the link between *Prdm9* and hybrid sterility. The trouble is that it's not obvious why two individuals who differ in their recombination hotspots might be sexually incompatible. Continuing research with mice may help to solve the problem by revealing the interactions between *Prdm9* and other genes. Although *Prdm9* seems to be key, no gene works entirely in isolation and the new research should give a better picture of what is going on at the genetic level. Forejt is close to pinpointing one such gene, located on the X chromosome, and there is another in the frame. Once these are better understood, it may be easier to understand whether, and how, *Prdm9* contributes to hybrid sterility in other species, including humans.

Earlier this year some intriguing findings came out. An analysis of 3200 people's genomes found a woman who was healthy and had children, but lacked the *Prdm9* gene. "This is a fascinating finding and unexpected. We will have to wait to see if other cases turn up," says McVean. He notes, though, that other species, including dogs, have been found to lack *Prdm9* and yet be fertile, so this is not without precedent.

If *Prdm9* does turn out to be some sort of universal reproductive-isolation gene in animals, that would be "beautiful", says Forejt. Then *Prdm9* would be a key to understanding how one species can split into two – Darwin's mystery of mysteries. The gene responsible for the seemingly innocuous process of genetic crossover truly would deserve to win the title of evolution's X factor. ■

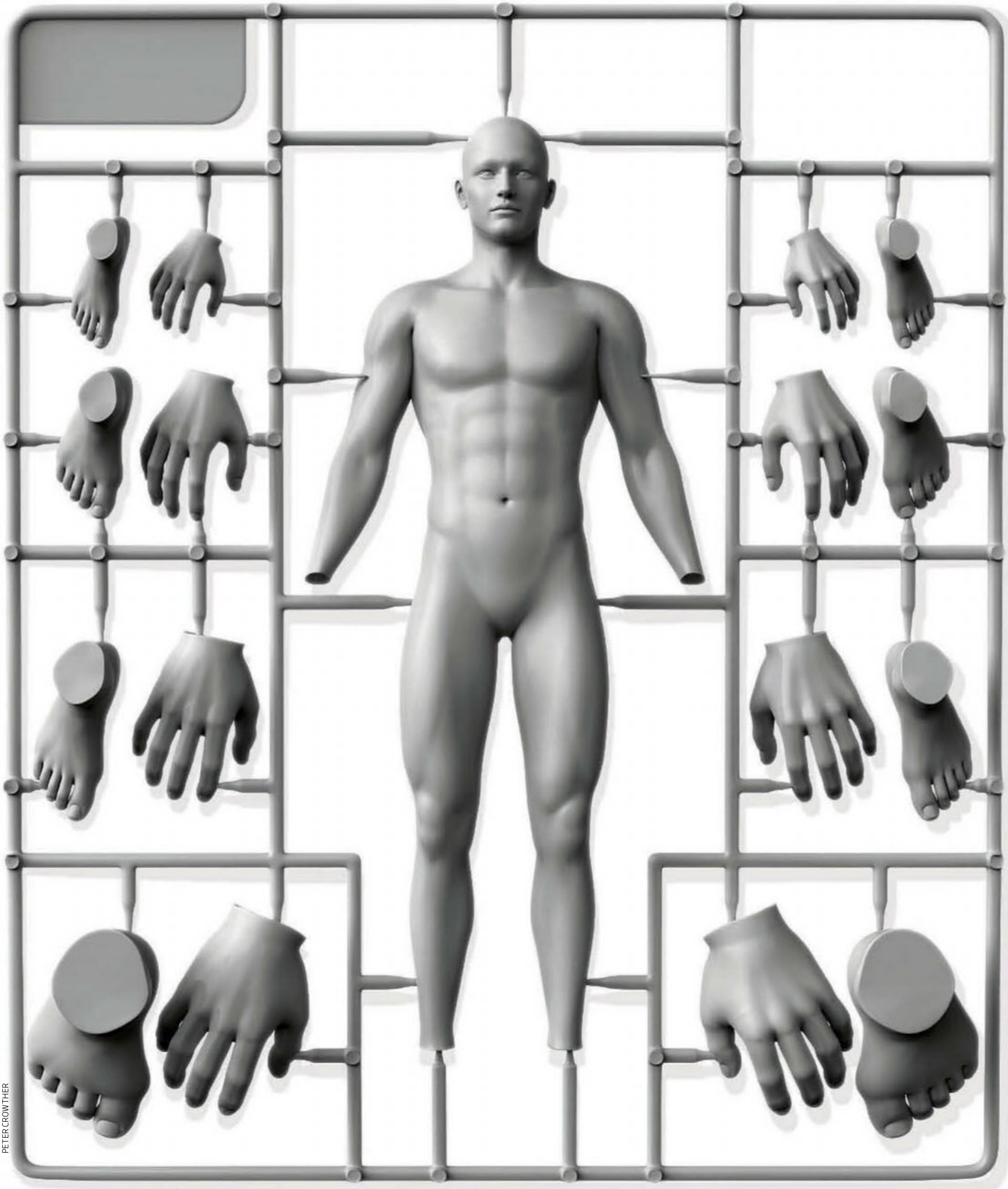
"It's not obvious why two individuals who differ in their recombination hotspots might be sexually incompatible"

WAYS TO SHUFFLE A GENOME

Whenever an animal produces an egg or sperm, it first shuffles the genetic pack in a process known as recombination (see diagram, opposite). This has the advantage of creating genetically diverse offspring, increasing the likelihood that at least some of them will survive. It is also what makes each of us – except identical twins – unique.

One surprising discovery is that some people do a more thorough job of shuffling than others. "There are people who recombine a lot before they hand their genomes to their offspring, and there are those who recombine little," says Kari Stefansson, CEO and founder of deCode Genetics in Reykjavik, Iceland. What's more, such differences extend to entire populations. For example, low levels of recombination are more common in people of African descent – who are more genetically diverse to begin with – than in Europeans. This suggests that evolution strikes a balance between the benefits of genetic diversity and the risk of introducing genetic errors through recombination.

Last year, Stefansson and his colleagues reported intriguing evidence that men and women, too, may have different recombination strategies. They used detailed genomic data from more than 15,000 parent-offspring pairs to track exactly where on the genome recombination events had occurred between the generations. They found that in women the crossover points tended to occur between genes, thus producing new combinations of genes. In men, the hotspots were slightly more likely to occur within spacer regions, or introns, which separate parts of a single gene, allowing recombination to create new versions of genes. No one knows why the two sexes should employ these different strategies but, once again, it looks as though males take the more risky approach even when it comes to shuffling their genetic pack.



PETER CROWTHER

Hidden forces are pushing and pulling on the levers of evolution. Dan Jones reports

Winning combinations

THE remarkable diversity of life on Earth stands as grand testimony to the creativity of evolution. Over the course of 500 million years, natural selection has fashioned wings for flight, fins for swimming, and legs for walking, and that's just among the vertebrates. The capacity for evolutionary innovation – or, in buzzword form, "evolvability" – is built into the fabric of life.

Can evolvability itself evolve, with species becoming more or less evolvable over time? And if so, what factors affect evolvability and can they be studied in the natural world? Few questions are more fundamental to evolutionary theory, yet evolvability didn't enter biological parlance until 1987, when arch-phrase-maker Richard Dawkins coined the term. In the intervening decades it has become a hot topic, though only recently has real-world evidence begun to put flesh on the bones of the theory.

Now there are studies aplenty to shed light on the factors that might constrain and enhance an organism's capacity to evolve. They are also explaining crucial events in human evolution, such as the switch to walking on two legs and the emergence of our highly dexterous, tool-using hands.

One of the first hurdles had been to define exactly what "evolvability" means. The aim is to capture the capacity of a species or population to respond to natural selection. Since genetic variation is the raw material on which selection acts, the extent of this variation in a population provides a crude measure of evolvability.

When most researchers talk about evolvability, however, they mean something more subtle – not just how much genetic variation is present, but whether this variation translates into adaptive changes in the organism's outward appearance and behaviour that could be shaped by natural selection. Günter Wagner, a pioneer in the field who is based at Yale University, therefore defines evolvability as "the capacity to generate heritable phenotypic variation". That is to say, variation in an organism's body-type that can be passed from generation to generation.

The real question, of course, is what determines this capacity. Two factors are key. Perhaps the most fundamental of these is an organism's "mutational robustness" –

> **"Evolutionary pressures on the feet might have prepared our hands for tool use and manual tasks"**

the capacity to develop normally despite the presence of genetic mutations. Since genes rarely act independently, a particular mutation could have a positive, negative or neutral effect on the organism, depending on the overall genetic background. Greater robustness could therefore be achieved by mechanisms that dampen the impact of mutations in any particular gene. In principle, that should increase an organism's survival because it reduces the chance of potentially harmful changes to the organism's body plan. But this buffering effect would also be the enemy of change, masking potentially beneficial variation and putting the brakes on the organism's evolvability.

Or so it might seem. In fact, by neutralising the effects of otherwise harmful mutations, robustness preserves genetic variations that might otherwise be weeded out. That means organisms accumulate a wealth of hidden mutations within the population. Further genetic or environmental changes might then remove the buffering mechanisms and unmask the effects of these stored mutations, providing ready-made variation in the organism's make-up. What might the mechanisms behind this robustness be?

The main players seem to be "heat-shock proteins", according to studies led by Susan Lindquist at the Massachusetts Institute of Technology. HSPs ensure that other proteins always fold in the same stable three-dimensional shape, which is vital for their role within the cell. Under harsh conditions like scorching temperatures or high salinity, proteins can fold wrongly, preventing them from carrying out their function. It is here that the HSPs step in, acting as chaperones to guide the protein into the correct shape and allowing it to function properly even under troublesome circumstances.

Crucially, HSPs also ensure a protein folds into the same stable shape even in the face of genetic mutations that shuffle the protein's sequence of amino acids. That permits hidden variation to build up over time without getting in the way of the protein's everyday activities.

The structure and function of proteins govern all kinds of processes in the development of an organism. So when

Lindquist's team knocked out the HSPs in thale cress and fruit flies, the stored mutations suddenly became apparent in physical changes to the organisms, including new leaf shapes for the cress and changes to the shape of the flies' eyeballs. The genes that code for HSPs don't routinely stop functioning in natural populations but occasionally changes to the environment, like a radical change in diet, can overwhelm the HSP system and lead to similar effects, providing variation that can respond to the new evolutionary pressures precisely when it is needed most.

SUPERSTOCK/GETTY

Lingering connections

HSPs are not the be-all and end-all of robustness. Some proteins are intrinsically more robust than others, even without the help of HSPs. This too can affect an organism's evolution. In 2006, for example, Jesse Bloom at the Fred Hutchinson Cancer Research Center, Seattle, and colleagues, showed that more robust proteins can pick up useful additional functions from new mutations without losing their basic structure and collapsing into a useless tangle. And in 2014, Bloom demonstrated that the ability of the influenza virus to tolerate mutations enables it to adapt to the pressure of immune system attack.

Other research led by Robert McBride, then at Yale University, showed that viruses bred to produce more robust proteins adapted to new evolutionary pressures, like higher temperatures, more quickly than less robust strains. In other words, they were more evolvable.

Robustness is only half of the story of evolvability, however. The second key factor concerns a phenomenon known as integration – the way different body parts or traits appear to vary and evolve together. Integration between traits often results from their shared evolutionary history. Body parts like limbs, teeth, ribs and vertebrae that are repeated along the body axis, for example, arose through the direct duplication of certain genes way back in evolutionary history. The two copies will not be completely independent of one another because the expression of both will ultimately be governed by the same regulatory genes at a different point in the genome, meaning the two body parts would still tend to vary and evolve together.

Integration is also likely if the different parts are involved in the same function. The four fingers and thumb, for example, work together for grasping and manipulation. To preserve the optimal use of the hand, changes in one part – a longer finger, say – need to be complemented by corresponding changes in the other digits. Selection therefore favours a developmental system in which genetic changes affecting digit length produce a coordinated shift in all digits.

"Environmental changes can unmask hidden mutations, providing ready-made variation when it's needed"

Like robustness, integration can be a double-edged sword. On one hand, it increases the capacity to generate coordinated, adaptive changes in body structures, which surely help to increase an individual's chances of survival. On the other, it also constrains the possible evolutionary avenues an animal could take – capping its evolvability, in other words – since a potentially beneficial change to one trait could have a disastrous impact on the other traits to which it is linked.

Luckily for life on Earth, integration is not an all-or-nothing affair. It is becoming clear that the traits can be integrated to varying degrees (see "Evolvable dogs", right). Sometimes existing integration can be uncoupled altogether, making each trait an independent "module" that is more evolvable.

Consider the evolution of wings in mammals. The fore and hindlimbs of mice and other rodents are very tightly integrated, so that changes in one limb pair, such as an increase in length, correlate almost perfectly with changes in the other pair, says James Cheverud, a biologist at Loyola University Chicago, who studied the link.

Bats, however, use their modified forelimbs for flying and their hindlimbs for grasping – two very different tasks, which would hint that the limbs are quite loosely integrated. Sure enough, Benedikt Hallgrimsson of the

The hindlimbs don't mind what the forelimbs get up to

University of Calgary, Canada, and Nathan Young of the University of California, San Francisco, found that the co-variation in the length of bones in the bat's fore and hindlimbs tends to be much lower than in other mammals. The implication is that the ancestors of bats must have lost the genetic integration between fore and hindlimbs somewhere along the evolutionary path, opening the door for the evolution of wings.

A similar story could explain various stages of primate evolution, too. Campbell Rolian at the University of Calgary, for example, has compared quadrupedal primate species such as macaques, in which the hands and feet share similar roles, with species like the great apes (humans, chimpanzees, gorillas and orangutans), in which the hands and feet perform independent functions.

As expected, Rolian found greater integration between the hands and feet of quadrupeds than in the great apes. Another analysis of the entire fore and hind-limb, rather than the individual hands and feet, found a similar result, with roughly 40 per cent less co-variation in the ape limbs compared with the quadrupeds.

The result was that "arms and legs could respond to natural selection with a greater degree of independence, thereby increasing their evolvability", says Hallgrimsson. Ultimately, this enabled early humans to evolve longer legs adapted to walking and running while leaving arm length relatively unchanged. By the same logic, a shortening of the forearm, which would have facilitated tool use, was not constrained by corresponding changes on the lower leg that might have reduced their walking power.

Importantly, integration comes in degrees. Even though the integration between the arms and legs has been significantly weakened over the years, some developmental connections linger that are strong enough to have changed the course of evolution in intriguing ways. For example, Rolian and Hallgrimsson, working with Daniel Lieberman of Harvard University, discovered that evolutionary pressures on the feet might have prepared humankind's highly dexterous hands for tool use and manual tasks. The team's discovery came from a detailed comparison of the length of the bones making up each toe and corresponding finger. They found that sufficient integration remain between the fingers and toes for them to have co-evolved to a certain degree.

Evolutionary pressures shaping the feet could therefore have changed the hands, or vice versa – but which way round? Using computer simulations to estimate the possible evolutionary pressures and corresponding changes to primate anatomy, the team suggests that natural selection acted primarily on the toes, enlarging the big toe and reducing the outer digits to stabilise the feet for walking.

The result, of course, was that as the big toe evolved, the thumb also grew accordingly. Completely by chance, that meant that the tips of the thumb and the fingers could now meet each other for the first time in evolutionary history, providing our ancestors with greater dexterity and precision gripping that became the key to the successful use of tools.

EVOLVABLE DOGS

The faces of man's best friend come in an astonishing range – from the short, squashed face of a Pekingese to the slender snout of a collie. Studies by Abby Drake, then at the University of Manchester in the UK, and her colleague Christian Klingenberg, have shown that diversity in dog faces is comparable to the diversity apparent between all carnivore species.

But the remarkable variation in dogs has been achieved in just a few thousand years of selective breeding, and was possible thanks to a limited integration between the face and brain – a lack not normally found in other mammals. Intriguingly, this modularity is also found in wolves, coyotes and jackals, suggesting dog faces were always this evolvable – they simply needed the right evolutionary pressures to shape their snouts.

Evolvability through the ages

The take-home message is that animals are made up of a "nested hierarchy" of modules and integrated traits, says Hallgrimsson. So while the bones of the arms and hands show reduced integration in humans (and great apes generally) compared with quadrupedal monkeys, integration was nonetheless strong enough between human hands and feet to have profound evolutionary consequences. It is these specific patterns of integration and modularity, rather than either factor independently, that ultimately determines evolvability, he says.

Indeed, looking deeper into prehistory, it is easy to see how these factors could have played a crucial role throughout animal evolution. About 540 million years ago, the Cambrian explosion led to the emergence of the basic body plans of the 35 or so phyla of animals recognised today. Their common ancestor had not achieved a high level of integration or robustness, making it developmentally flexible and primed for evolutionary innovation. Evolution cashed in on that flexibility but soon pushed for greater developmental integration, more or less fixing the 35 body plans in the process.

That's not to say evolvability has taken a nosedive since then. Although the developmental processes that produce the basic body plans of animals are too tightly integrated for fundamental change, a further drive towards greater modularity among parts of animals has increased their individual evolvability. It is this tinkering with bits and pieces of animal bodies, rather than radical reinvention of the body, that has fuelled the astonishing biological innovation among arthropods and vertebrates in particular.

Finding out exactly what triggers the dissociation of integrated traits, prompting them to become increasingly modular, is now a key goal. It is possible that, in some cases, body parts become dissociated as a lucky accident that evolution then capitalises on. Getting a better handle on the process of dissociation requires a deeper understanding of the genetic mechanisms involved. Cheverud's lab has already made steps in this direction by mapping genes that determine the integration among various characteristics in mice. But the genetic detective work is revealing a complex picture. For example, a huge number of gene variants are implicated in determining the facial shape of humans, says Hallgrimsson. "You can't explain a lot of the variation from the genomic data. So many complex traits are turning out to be like that." Changes in the way genes are regulated, rather than changes in the genes themselves, is key. Intriguingly, other research has found that evolvability itself is evolvable.

These are early days in the empirical study of evolvability. Further progress will depend on researchers drawing together data on diverse aspects of biology, says Christian Klingenberg, a biologist at the University of Manchester in the UK. A complete theory of integration, modularity and the developmental basis of evolvability will require connecting genetics and developmental biology with morphological studies in both experimental and natural settings. It will be a hard slog but, as Klingenberg says, "it's where the fun starts". ■

Adapt first, mutate later

Evolution is meant to start with random mutations. But we may have things the wrong way round, reports Colin Barras

MORGAN SCHWEITZER

"TO BE honest, I was intrigued to see if they'd even survive on land," says Emily Standen. Her plan was to drain an aquarium of nearly all the water and see how the fish coped. The fish in question were bichir fish that can breathe air and haul themselves over land when they have to, so it's not as far-fetched as it sounds.

What was perhaps more questionable was Standen's rationale. Two years earlier, in 2006, *Tiktaalik* had become a global sensation. This 360-million-year-old fossil provides a snapshot of the moment our fishy ancestors hauled themselves out of the water and began trading fins for limbs. Standen thought forcing bichir fish to live almost entirely on land could reveal more about this crucial step in our evolution. Even if you were being kind, you might have described this notion as a little bit fanciful.

Today, it seems positively inspired. The bichirs did far more than just survive. They became better at "walking". They planted their fins closer to their bodies, lifted their heads higher off the ground and slipped less than fish raised in water. Even more remarkably, their skeletons changed too. Their "shoulder" bones lengthened and developed stronger contacts with the fin bones, making the fish better at press-ups. The bone attachments to the skull also weakened, allowing the head to move more. These features are uncannily reminiscent of those that occurred as our four-legged ancestors evolved from *Tiktaalik*-like forebears.

What is really amazing about this experiment is that these changes did not come about after raising generations of fish on land and allowing only the best walkers to breed. Instead, it happened within the lifetime of individual fish. Simply forcing young fish to live on land for eight months was all it took to produce these quite dramatic changes.

We have long known that our muscles, sinews and bones adapt to cope with whatever we make them do. A growing number of biologists think this kind of plasticity may also play a key role in evolution. Instead of mutating first and adapting later, they argue, animals often adapt first and mutate later. Experiments like Standen's suggest this process could even play a role in major evolutionary transitions such as fish taking to land and apes starting to walk upright.

The idea that plasticity plays a role in evolution goes back more than a century. Some early biologists thought that characteristics acquired during an animal's lifetime could be inherited by their offspring: giraffes got their long necks by stretching to eat leaves, and so on. The French naturalist Jean-Baptiste Lamarck is the best-known advocate of this idea, but Darwin believed something similar. He even proposed an elaborate mechanism to explain how information about changes in the body could reach eggs and sperm, and therefore be passed on to offspring. In this way, Darwin suggested, plasticity produces the heritable ›

variations on which natural selection can work its magic.

With the rise of modern genetics, such notions were dismissed. It became clear that there is no way for information about what animals do during their lifetime to be passed on to their offspring (although a few exceptions have emerged since). And it was thought this meant plasticity has no role in evolution.

Instead, the focus shifted to mutations. By the 1940s, the standard thinking was that animals mutate first and adapt later. A mutation in a sperm cell, say, might produce a physical change in the bodies of some offspring. If the change is beneficial, the mutation will spread through the population. In other words, random genetic mutations generate the variation on which natural selection acts. This remains the dominant view of evolution today.

The dramatic effects of plasticity were not entirely ignored. In the 1940s, for instance, the Dutch zoologist Everhard Johannes Slijper studied a goat that had been born without forelegs and learned to hop around, kangaroo-like, on its rear legs. When Slijper examined the goat after its death, he discovered that the shape of its muscles and skeleton looked more like those of a biped than a quadruped.

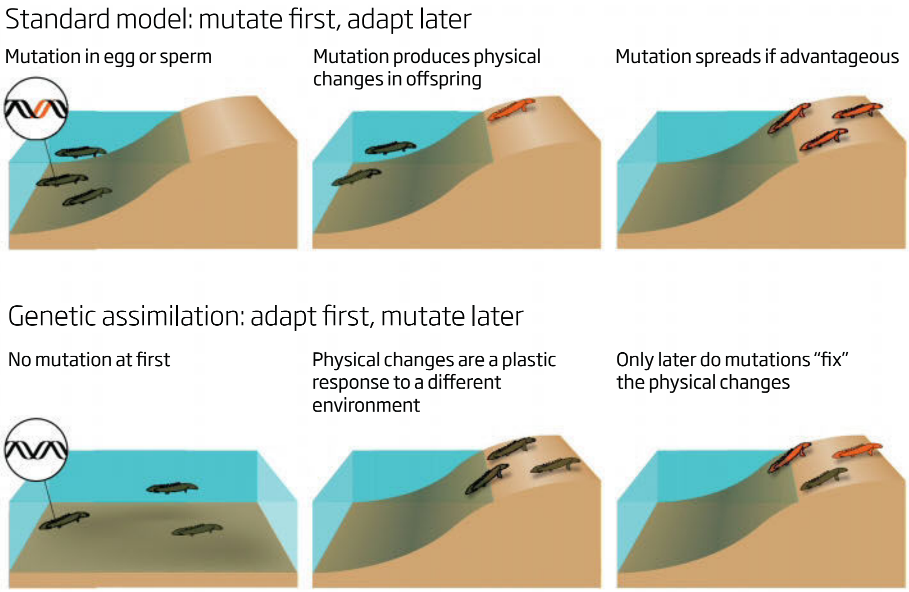
Few biologists considered such findings relevant to the evolutionary process. The fact that changes acquired during an animal's lifetime are transient seemed to rule out that possibility. If Standen's better-at-walking fish were bred and the offspring raised in a normal aquarium, for instance, they should look and behave like perfectly ordinary bichirs.

Transient response

But what if the environmental conditions that induce the plastic response are themselves permanent? In the wild, this could happen as a result of alterations in prey animals, or in the climate, for instance. Then all the members of a population would develop in the same, consistent way down the generations. It would look as if the population had evolved in response to an altered environment, but technically it's not evolution because there is no heritable change. The thing is, the only way to tell would be to "test" individuals by raising them in different circumstances.

In this way at least, plasticity can allow animals to "evolve" without evolving. The crucial question, of course, is whether it can lead to actual evolution, in the sense

Evolving without evolving



of heritable changes. "You can plastically induce generation after generation," says Standen, who is now at the University of Ottawa in Ontario, Canada. "At some point, can you remove the environmental conditions that induced the change and have the organisms remain changed?"

The answer, surprisingly, seems to be yes. In the 1950s, British biologist Conrad Hal Waddington showed that it is feasible in an experiment involving fruit flies. Waddington found that when pupa are briefly heated, some offspring develop without crossveins in their wings. He then selected and bred those flies. By the 14th generation, some lacked crossveins even when their pupa were not heated. A physical feature that began as a plastic response to an environmental trigger had become a hereditary feature.

How is this possible? Plastic changes occur because an environmental trigger affects a developmental pathway in some way. More of a certain hormone may be produced, or produced at a different time, or genes are switched on that normally remain inactive, and so on. The thing is, random mutations can also have similar effects. So in an environment in which a particular plastic response is crucial for survival, only mutations that reinforce this response, or at least do not impede it, can spread through a population. Eventually, the altered developmental pathway will

No coincidence

Can plasticity explain why evolution repeats itself?

During the last ice age, great ice sheets covered much of Eurasia and North America. As they retreated, they left behind lakes and rivers with no native fish.

Marine three-spined sticklebacks were quick to take advantage, repeatedly colonising these new environments and evolving into the freshwater sticklebacks found today (pictured right). What's extraordinary, though, is that freshwater species that evolved entirely independently of each other are often strikingly similar in body shape, and so on.

This is far from the only example. The cichlid fish of Africa's lakes, for instance, have also evolved along parallel lines in many cases.

The standard explanation for this is convergent evolution: even though mutations are random, similar environments produce similar evolutionary results. And there is some evidence to support this view, for instance when it comes to the loss of armour plates

become so firmly stabilised by a genetic scaffolding that it will occur even without the environmental trigger, making it a permanent hereditary feature.

Waddington called this process genetic assimilation. It may sound like Lamarckism, but it is not. The acquired characteristics don't shape the genetic changes directly as Darwin proposed, they merely allow animals to thrive in environments that favour certain mutations when they occur by chance.

Waddington's findings have been regarded as a curiosity rather than a crucial insight. But in the past decade or two, attitudes have begun to change. One reason for this is a growing appreciation of the flexibility of genes. Rather than being rigidly preprogrammed, we now know that the environment influences many aspects of animals' bodies and behaviour.

Such discoveries have led some biologists to claim that developmental plasticity plays a major role in evolution. A few, such as Kevin Laland at the University of St Andrews, UK, even argue that the conventional "mutate first, adapt later" picture of evolution needs a rethink. Most biologists have yet to be convinced.

The sceptics point out that genetic assimilation does not overturn any fundamental principles of evolution – in the long run, evolution is all about the spread of mutations, whether or not plasticity is

"The 'bipedal' mice had features like those in our hominin ancestors"

involved. Yes, say the proponents of plasticity, but the key point is that plasticity can determine which mutations spread, so its role should be given the prominence it deserves. "Several major recent evolutionary textbooks do not even mention plasticity," says Laland.

It may play a role occasionally, respond the sceptics, but it's a minor one at best. "There is little debate that genetic assimilation can happen," says Gregory Wray of Duke University in Durham, North Carolina. "But there is unfortunately very little support for its role in nature." This is what makes Standen's work on the bichir so significant. It implicates plasticity in a major evolutionary transition: fish turning into four-legged land animals.

Plasticity will soon be implicated in another major transition too – the one our ancestors made from four legs to two about 7 million years ago. Adam Foster, now at the Northeast Ohio Medical University in Rootstown, has been making rats walk on a treadmill. "I had a custom harness system built so I could modify the load experienced by the hind limbs," he says. Some rats had to walk on their hind limbs, while others walked on all fours. Each rat exercised on the treadmill for an hour a day for three months, and then Foster examined their skeletons.

He found that the "bipedal" rats had developed longer legs than standard quadrupedal rats, and that their thigh bones had larger femoral heads – the ball ›

in freshwater stickleback species.

But Mary Jane West-Eberhard of the Smithsonian Tropical Research Institute in Costa Rica thinks parallel evolution happens too often for convergence to be the full explanation. In her 2003 book *Environmental Plasticity and Evolution,* she argues that it happens because similar conditions produce a similar plastic response in the ancestral species. Natural selection then reinforces those trajectories.

If West-Eberhard is right, then at least some of the heritable characteristics seen in living animals originated from the plastic changes that occurred as their ancestors moved into new environments. And this is actually a testable prediction when it comes to freshwater sticklebacks; marine three-spined sticklebacks are still around, and have changed little since the ice age.

So Matthew Wund at The College of New Jersey in Ewing decided to put West-Eberhard's ideas to the test. With colleagues at Clark University in Worcester, Massachusetts, he set out to discover whether simply allowing marine sticklebacks to eat a diet similar to those of their freshwater cousins as they grew up would lead them to develop similar body shapes too. And it did.

Marine fish raised on planktonic invertebrates from the upper water of deep lakes developed the long snouts of sticklebacks living in lake surface waters. In contrast, marine fish given large invertebrates found at the bottom of shallow lakes developed the stubby snouts typical of sticklebacks that live there.

"We subsequently expanded the experiment to consider not only dietary differences but also habitat," says Wund. The results of those experiments, published a couple of years ago, also support the idea that developmental plasticity shaped the evolution of sticklebacks as they invaded the lakes left by the retreating ice sheets.

SIMON BOOTH/SCIENCE PHOTO LIBRARY

in the hip joint. Both features are associated with the transition to bipedalism in our hominin ancestors. "I think Adam's research is really compelling," says Jesse Young, an anatomist at Northeast Ohio Medical University. "As he was getting it going, I was a bit sceptical. You couldn't predict it would reveal anything useful."

While the work of Standen and Foster suggests that developmental plasticity could play a role in major evolutionary transitions, it is only suggestive. Indeed, these studies do not even show that the plastic changes seen in the bichir fish and mice can be fixed by mutations. Demonstrating this kind of genetic assimilation would certainly be tricky, says Standen. It would not be practical with the bichir fish she studied. "As wonderful as they are, they're frustrating fish," says Standen. "They take the better part of a decade to mature, and even then they're really difficult to breed in captivity."

The fossil record is usually no help either. It is possible that some of the changes seen as fish colonised the land were a result of plasticity rather than genetics, says Per Ahlberg of the University of Uppsala in Sweden who studies the transition to land. For Ahlberg, the trouble is that there is no way to prove it. "There's no evidence that will allow us to choose between the two," he says.


TOBIAS BERNHARD/GETTY

Fiddler crabs can take either side in the debate about the role of plasticity

More evolvable

Other biologists are more enthusiastic. It has long been suggested that different parts of the skeleton are more plastic and "evolvable" than others, says William Harcourt-Smith of the American Museum of Natural History. "So a foot bone or a hand bone might give you more useful info than a hip bone, for instance."

Work like Foster's could reveal if this is indeed the case and help us interpret the fossil record of human evolution. "These experiments do have validity," Harcourt-Smith says. "They can help us understand whether traits are plastic or not."

Take the honeycomb structure in the heads of our long bones. It is lighter and weaker than it was in our extinct cousins such as the Neanderthals. A study out last year compared the bones of hunter-gatherers and early farmers in North America. It concluded that our bones became weak only when our ancestors' lifestyles changed. "We could have a skeleton as strong as our prehistoric ancestors," says team member Colin Shaw of the University of Cambridge, UK. "We just don't because we're not as active."

It's possible that similar kinds of skeletal structural change seen in prehistory have been misinterpreted as signs of speciation when they really just reflect developmental plasticity, says Shaw – perhaps especially so in hominin evolution. Humans are unique, he points out. "Our first line of defence against environmental insult is culture. When that's not adequate – for instance if the clothing you can make is not good enough to keep you warm – then arguably the second line of defence is plasticity. Only after that fails might you actually get genetic selection."

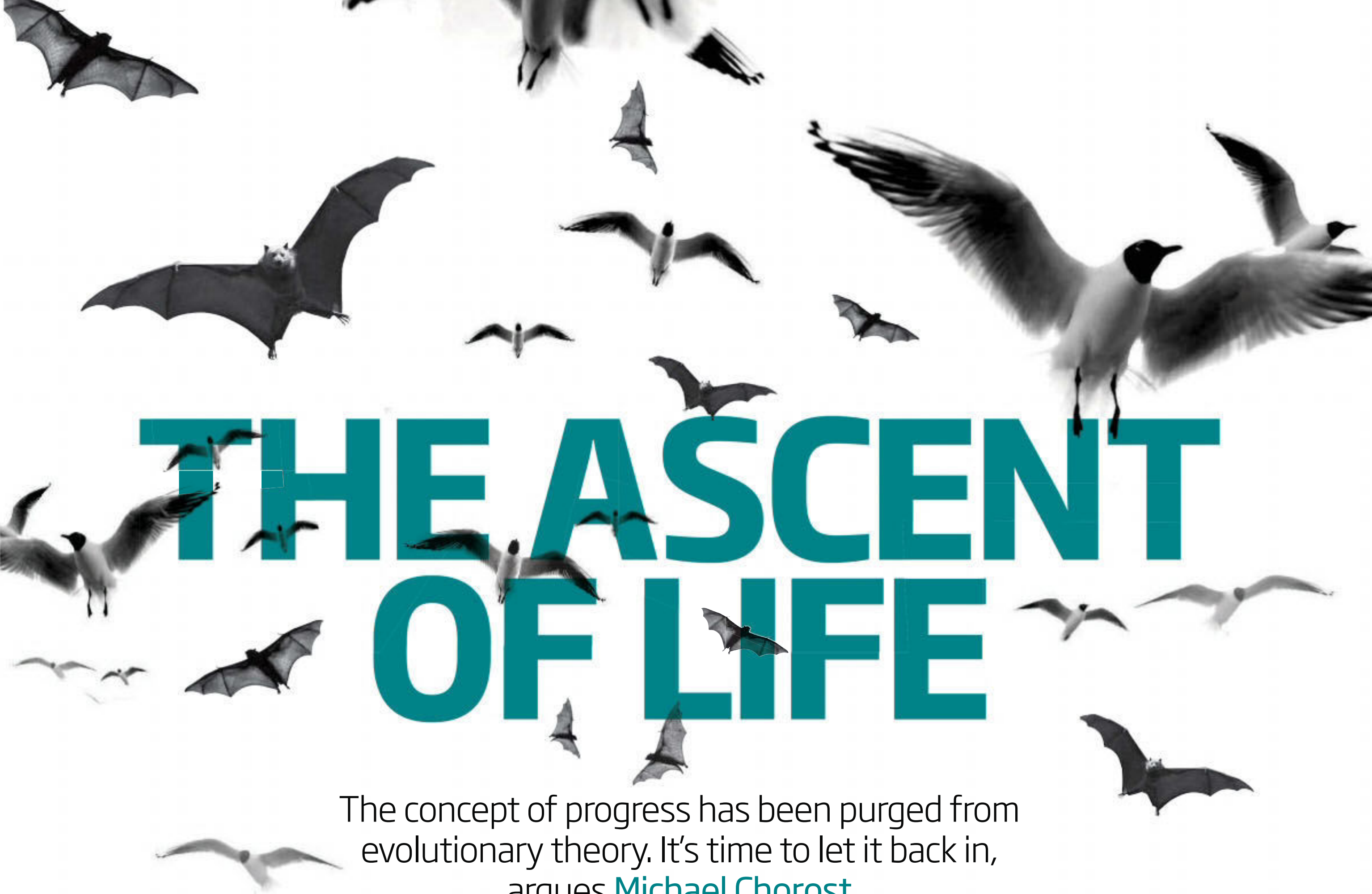
All this still leaves open the question of whether genetic assimilation can "fix" traits that first appear as a result of plasticity. A decade ago, Richard Palmer at the University of Alberta in Edmonton, Canada, found a way to search for evidence in the fossil record. Most animals have some asymmetric traits. In our case, it's the position of the heart and other organs, which is encoded in our genes. But in other species, asymmetries are plastic. For instance, the enlarged claw of male fiddler crabs (pictured above) is as likely to be on the left as on the right.

What Palmer showed by examining the fossil record of asymmetry in 68 plant and animal species is that on 28 occasions, asymmetries that are now hereditary and appear only on one side started out as non-hereditary asymmetries that appeared on either side. "I think it's one of the clearest demonstrations that genetic assimilation has happened and that it is more common than expected," says Palmer.

There is a caveat here, though. The ancestral non-hereditary asymmetries may have been a result of random genetic noise, says Palmer. So while his work does show genetic assimilation in action, it was not necessarily fixing traits due to developmental plasticity.

There is no simple way to prove the evolutionary importance of developmental plasticity, says Mary Jane West-Eberhard of the Smithsonian Tropical Research Institute in Costa Rica, whose work has been particularly influential. "Evolutionary biology that is concerned with evolution and speciation in nature necessarily depends on indirect proof – an accumulation of facts that support or deny a hypothesis," she says.

At the moment, the facts that are accumulating seem to support the hypothesis. Expect lots more results soon: Standen's success is inspiring others. "I've already had people ask me what other critters we could try this on," says Standen. "Everybody is friendly and excited and interested. It's fun – it's the way science should be." ■



GETTY; FRANS LANTING NGS; JASON HOBBS / MILLENNIUM IMAGES, UK

THE ASCENT OF LIFE

The concept of progress has been purged from evolutionary theory. It's time to let it back in, argues Michael Chorost

CELEBRATED palaeontologist Stephen Jay Gould once wondered what would happen if we could rewind the tape of life. If it were possible to turn the clock back half a billion years and then let evolution happen all over again, what would we see? Gould famously argued that the history of life would not repeat itself. The world would be unfamiliar, and would probably lack humans.

His point was to demonstrate that evolution is not a process of inexorable progress but of contingency. Mutations happen unpredictably. Sexual reproduction combines genes at random. Droughts, ice ages and meteorites strike without warning and kill off fully fit individuals and species.

We tell ourselves stories of evolutionary progress but these are just wishful thinking. Life produces abundant variations; most fail. The few that survive we call the most advanced, but that is a profound error which conflates "latest" with "best". As Gould wrote in his classic book *Wonderful Life:* "Life is a copiously branching bush, continually pruned by the grim reaper of extinction, not a ladder of predictable progress".

Gould also had little time for humanity's hubris. Far from being the pinnacle of evolution, we are just another product of contingency. "Perhaps," he wrote frostily, "we are only an afterthought, a kind of cosmic accident, just one bauble on the Christmas tree of evolution."

Gould's view is the orthodoxy of evolutionary theory. Yet it remains hard to reconcile with the intuitive sense that life has indeed progressed over time. All life was once single-celled, yet now a single organism can contain tens of trillions of cells. The number of cell types has increased, too, from one kind in single-celled organisms to 120 in mammals. Brains have grown larger. And humans have accelerated this trend in the past 50,000 years with our own uneven but powerful ascent.

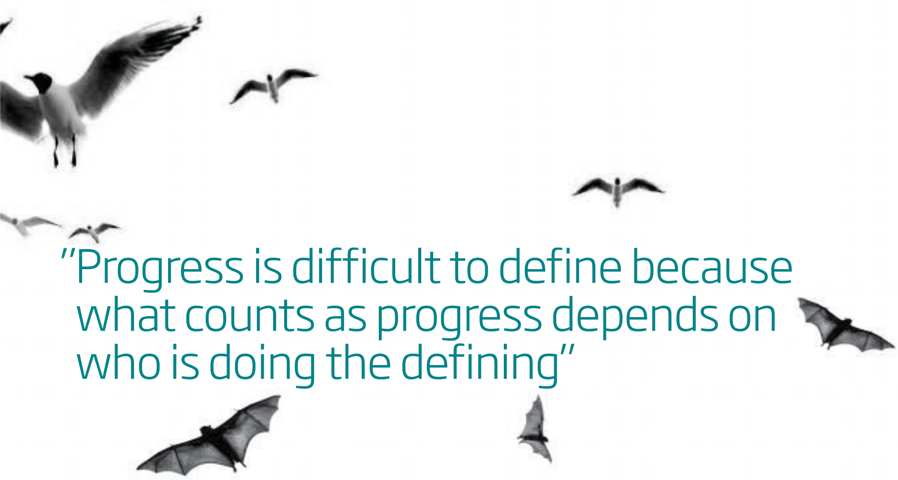
> "We tell ourselves stories of evolutionary progress but these are just wishful thinking"

For many years, a small but energetic group of researchers has been trying to rehabilitate the concept of evolutionary progress and explain it in theoretical terms. They hope to show that Gould's view of evolution is too bleak and that certain kinds of biological progress are not merely accidental or illusory, but necessitated by physical law. If these researchers succeed, it could lead to a crucial modification of current theory.

Gould and those who followed in his footsteps accepted that life has increased in size, complexity and diversity. However, they argue that this is not because evolution is inherently progressive.

Instead, it is an illusion. By definition the first life was very simple. As variation increased, some organisms inevitably became more complex. Humans pay the most attention to the complex ones, leading to a belief in an upward march. As Sean B. Carroll, a professor of molecular biology at the University of Wisconsin-Madison, puts it: when there is nowhere to go but up, some species will go up.

Development-oriented theorists accept these passive increases in complexity. ›



"Progress is difficult to define because what counts as progress depends on who is doing the defining"

SEAN DAVEY/PLAINPICTURE

But they argue that there are also "driven" processes that bias evolution toward increasing complexity. John Smart, a member of the evolution, complexity, and cognition research group at the Free University of Brussels in Belgium and a leading thinker in this field, argues that evolution and development can be reconciled. That is, it will be possible to define progress in objective terms and explain why it must happen. The case laid out by Smart and other theorists is based on at least four arguments.

The first concerns a new way of thinking about progress – a concept that is notoriously difficult to define, largely because what counts as progress depends on who is doing the defining. More complexity seems valuable to us, for example, but many organisms – especially parasites – are successful thanks to a reduction in complexity.

Energy flows

Rooting a new definition in basic physics would be one way around this problem. Eric Chaisson, an astrophysicist at Harvard-Smithsonian Center for Astrophysics, Cambridge, Massachusetts, has put forward the idea of energy rate density, a measure of how much energy flows through each gram of a system per second. A star, for all its spectacular output, has a much lower energy rate density (2 ergs per gram per second) than a houseplant (3000 to 6000 ergs per gram per second). This sounds counter-intuitive until you remember that stars are just balls of gas.

Humans do better still, with a basic energy rate density of 20,000 ergs per gram per second. Societies, too, can be measured in this way. Chaisson estimates that hunter-gatherer societies have an average energy rate density of 40,000 ergs per gram per second, while technological societies use 2 million ergs per gram per second.

Chaisson argues that energy rate density is a universal measure of the complexity of all ordered systems, from planets and stars to animals and societies. Furthermore, when he plots the energy rate density of such ordered systems against the time they first appear in the history of the universe, the line goes unequivocally upwards, indicating a general increase in complexity over time (see graph, below).

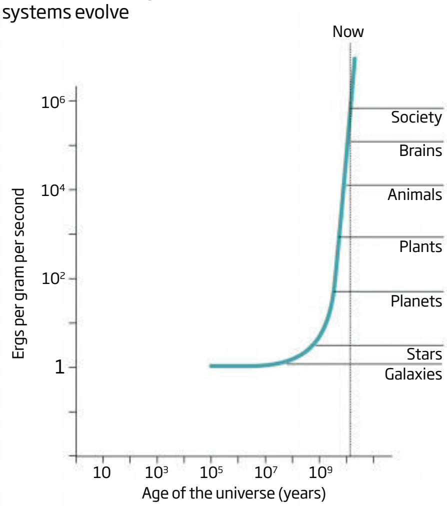
The second argument concerns thermodynamics. At first sight, the second law of thermodynamics is a gloomy affair. It seems to indicate that increases in disorder are inevitable and irreversible and that the universe is running out of the energy needed to create and sustain complex entities such as living things.

A literal reading of this law implies that the ascent of life is extremely unlikely. More nuanced readings, however, have been used to argue that local increases in complexity are not merely permitted by the law, but required by it, and order can and does emerge spontaneously from chaos.

Physicist J. Miguel Rubí of the University of Barcelona in Spain says that, strictly speaking, the second law of thermodynamics applies only to systems in equilibrium, a state in which nothing changes. This condition is rarely

Growing energy density

As the universe ages, ever more complex systems evolve

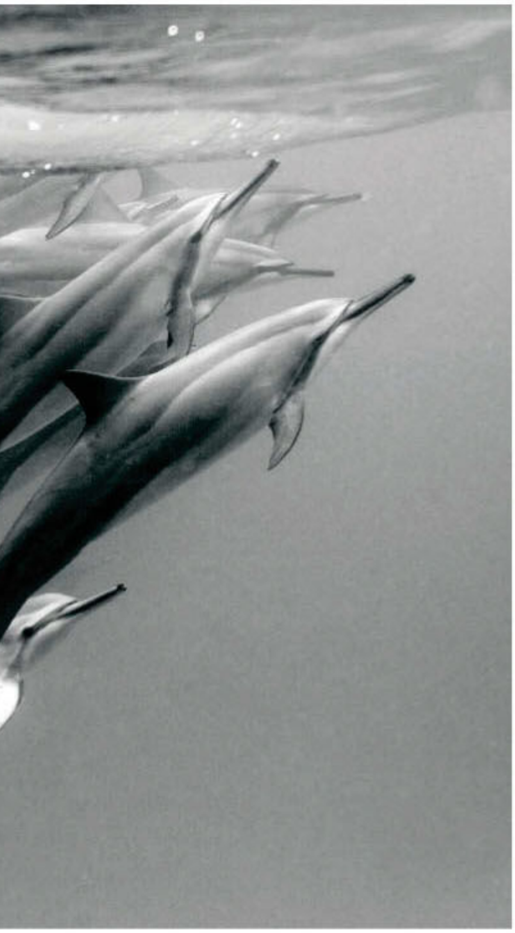


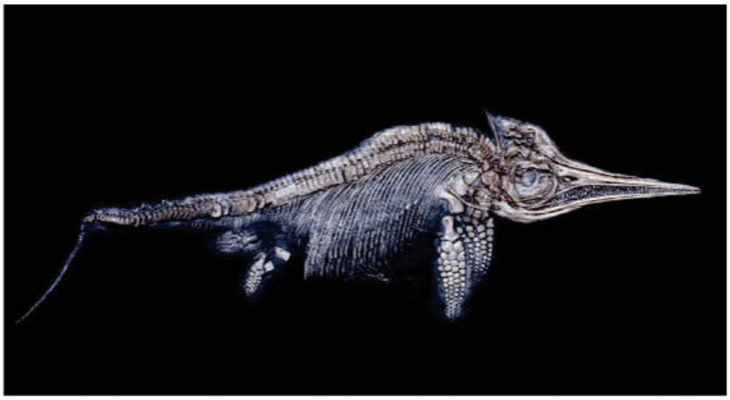
SOURCE: CHAISSON

present in the universe. Earth, for example, is heated by the sun, creating energy gradients on its surface. Where energy gradients exist, pockets of complexity can arise even as the system as a whole decays into disorder. These pockets provide a foothold for further increases in complexity. Energy gradients thus provide a loophole in the second law that permits life to arise and ascend.

Argument number three is convergent evolution. Taking a different view to Gould's argument, the tape of life has been rerun many times – at least partially. In many cases, very different species living in similar environments have independently evolved in similar ways.

In his book *What Technology Wants*, Kevin Kelly, the founding editor of *Wired* magazine, gives numerous examples of convergent evolution to support his argument that the outcomes of evolution – of which he considers technology one – are not accidental. Flapping wings evolved independently in birds, bats and pterodactyls. Dolphins, bats and several species of cave-dwelling bird separately hit on echolocation. Fish in the Arctic and the Antarctic independently evolved antifreeze compounds. Perhaps the best-known example is the camera eye, which has evolved independently at least





NATURAL VISIONS / ALAMY

Convergent evolution, as seen in ichthyosaurs and dolphins, may suggest inevitable patterns in life

six times. The implication, Kelly writes, is that many outcomes of evolution are not accidental but inevitable. These outcomes include not just organs but brains, minds, societies, and technologies.

Intelligence may be another convergent property. Nicola Clayton, a professor of comparative cognition at the University of Cambridge, and Nathan Emery, a cognitive biologist at Queen Mary, University of London, argue that while primates and crows are far apart on the evolutionary tree and have very different brain structures, they have independently evolved many similar kinds of cognition, including tool use, deception and complex social groupings. The implication, again, is that intelligence always emerges in favourable conditions.

Last of all, a theory of development must account for catastrophism. The occurrence of unpredictable, planet-altering events is a challenge for any developmental perspective on evolution. Had the dinosaurs not been killed by an impact, critics of the theory say, mammals would not have had the opportunity to expand into new niches and there would have been no evolutionary sequence leading from primates to tool-wielding, language-using apes. In short: no impact, no us.

Simon Conway Morris, a palaeontologist at the University of Cambridge, counters this by arguing that while catastrophes delay or accelerate the developmental process they do not significantly change it. The key is convergent evolution.

Hold the extinction

Suppose the deadly meteorite had sailed harmlessly by, Conway Morris suggests. The dinosaurs would have survived for the next 30 million years until Earth's next glaciation. The cold would have killed off those dinosaurs living north and south of the tropics, opening up niches for the warm-blooded mammals and birds that co-existed with them. Eventually tool-users not unlike us would have evolved and sooner or later any dinosaurs remaining in the tropics would have been hunted to extinction. "The mass extinction of the dinosaurs would then have been under way, perhaps 30 million years behind schedule in comparison with the real world," he writes.

So whatever catastrophe hits, the tape of life would probably run more or less the same way. It might delay the developmental process by reversing an advance, but the advance would eventually happen again. Or it might accelerate the process by opening up an environmental niche. In either case, the outcome would not change substantially; only the timing would.

If these four arguments hold up, it would mean a significant expansion of evolutionary theory is needed, showing that life not only evolves, it develops.

The implications would be profound. Development, unlike evolution, has a direction: an acorn becomes a tree, an embryo becomes a newborn. It never goes the other way. And while the outcome is not fully determined, it is powerfully constrained.

Direction and constraint, however, do not imply design and purpose. A developmental view of evolution needs no help from teleology. Such a theory of evolution offers no support for intelligent design. Indeed, it would strike another major blow to it by offering a cogent naturalistic explanation for the emergence of complexity.

Perhaps more profoundly, admitting progress into evolution would give a different perspective on our own existence. In offering a naturalistic explanation for the emergence of intelligence and its offspring, language and technology, it would cast them as predictable outcomes of the cosmos rather than as accidents of contingency. Far from being "just one bauble", we would have an explicable, even inevitable, place in the order of things. ■

"Whatever catastrophe hits, the tape of life would probably run more or less the same way"

Unnatural selection

Humans have become the biggest force in evolution, as **Michael Le Page** discovers

THE Zoque people of Mexico hold a ceremony every year during which they grind up a poisonous plant and pour the mixture into a river running through a cave (pictured below). Any of the river's molly fish that float to the surface are seen as a gift from the gods. The gods seem to be on the side of the fish, though – those in the poisoned parts of the river are becoming resistant to the plant's active ingredient, rotenone.

If fish can evolve in response to a small religious ceremony, just imagine the effects of all the other changes we are making to the planet. We are turning grassland and forests into fields and cities, while polluting the air and water. We are hunting species to the brink of extinction and beyond, as well as introducing new pests and diseases to just

JAIME AVALOS/EPA/CORBIS

Even a small religious ritual can trigger rapid evolution

about every part of the world. And that's not to mention drastically altering the climate of the entire planet.

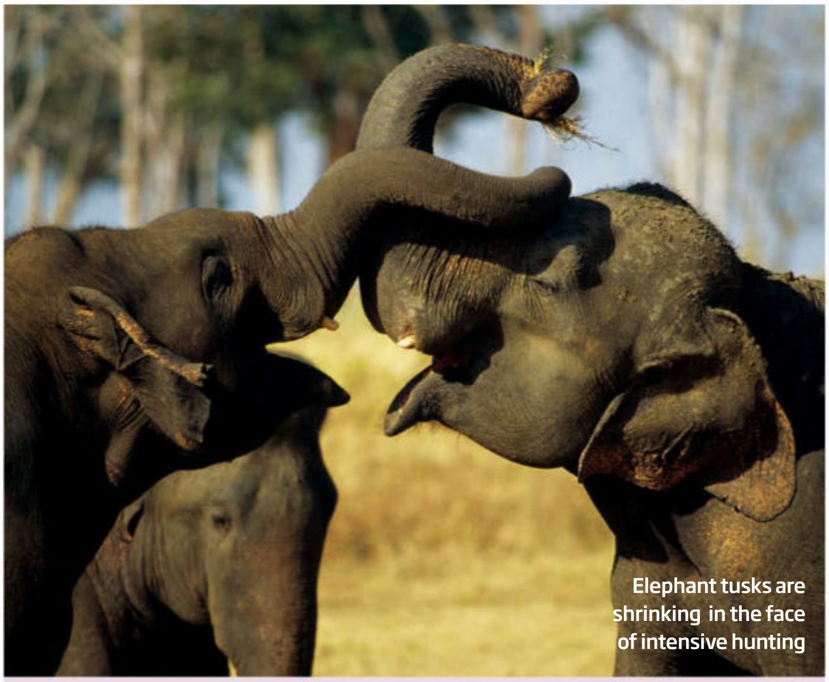
It is no secret that many – perhaps even most – species living today are likely to be wiped out over the next century or two as a result of this multiple onslaught. What is now becoming clear is that few of the species that survive will live on unchanged.

Far from being a slow process, evolution can occur extremely rapidly when the environment changes (see "In the fast lane", page 86). So, as we alter the planet ever faster and more drastically, we are becoming the main force driving evolution. "The intensity of the ecological effect of man is pretty obvious," says Stephen Palumbi of Stanford University in California. "There is an amazing amount of evolutionary change as a result."

Some of the fastest rates of evolution ever measured in the wild are in plants and animals harvested by humans. The few populations for which we have data are, on average, evolving three times as fast as populations subject only to natural pressures, for example.

Over the following pages, we look at the many ways in which plants and animals are already evolving in response to human pressures. Some of these changes, such as animals evolving to survive in highly polluted areas, can be seen as a positive thing. Others are bad from our point of view, such as animals we hunt losing the traits we value most in them, or pests becoming immune to poisons. What is clear is that whether the issue is growing enough food, conserving wild animals or keeping our beds bug-free, human-driven evolution is a factor we can no longer afford to ignore. ›

"Many species will be wiped out over the next century. Of the ones that survive, few will live on unchanged"


JASON EDWARDS/NGS

Elephant tusks are shrinking in the face of intensive hunting

Hunting

Most predators target the young or the weak. We are different, targeting the biggest and best, or those with characteristics we desire, such as large antlers. Combine this with our ability to kill in great number and the result is extremely rapid evolution of our prey.

The first clear evidence was published in 1942, and since then many examples have emerged of how hunting can transform the hunted. The targeting of large animals has resulted in a fall in the average size of caribou in some areas, for instance, while trophy hunting has led to bighorn sheep in Canada and mouflon in France evolving smaller horns.

Perhaps the most dramatic example is the shrinking of tusks in elephants, or even their complete loss. In eastern Zambia, the proportion of tuskless female elephants shot up from 10 per cent in 1969 to nearly 40 per cent in 1989 as a result of poaching. Less dramatic rises in tusklessness have been reported in many other parts of Africa, with some bull elephants losing tusks too.

Humans have had an even bigger impact in Asia. Only male Asian elephants have tusks, and the proportion of tuskless bulls has soared in many areas. In Sri Lanka, where there has been a lot of poaching, under 5 per cent of males now have tusks, says Raman Sukumar of the Indian Institute of Science in Bangalore, who studies Asian elephants. Simulations by Ralph Tiedemann of the University of Potsdam in Germany and colleagues suggest that female elephants' preference for tuskers has partly counteracted the effect of hunting. However, even if all poaching stopped, it would take a very long time for the percentage of tuskers to rise again.

It's not just animals that are being shaped by human preferences: the harvesting of wild plants can have a similar effect to hunting and fishing. In Tibet, for example, the height of the snow lotus at flowering has nearly halved over the past century as a result of the flowers being picked for use in traditional medicine.

To even the balance, some biologists are now promoting the idea of counteracting the evolutionary pressures of hunting through "compensatory culling" – killing animals with undesirable traits. This has actually long been done in some places. In Germany and Poland, for instance, there is a tradition of shooting yearling deer with poor antlers to prevent a decrease in the antler size of mature stags.

Private reserves in countries such as Zimbabwe have a similar policy. They typically charge hunters a smaller "trophy fee" for shooting tuskless elephants – $3000 versus at least $12,500 for a tusker, for example. This is partly because tuskless animals are less valuable, but it is also a deliberate attempt to eliminate the trait.

TUI DE ROY/MINDEN PICTURES/FLPA

Many lizard species face extinction in the hotter climate of the future

Warming the planet

In Finland, the tawny owl used to be mainly grey. But since the 1960s, the proportion of a brown subtype has risen fast. "The frequency averaged around 12 per cent in the early 60s and has increased steadily to over 40 per cent nationwide," says Patrik Karell of NOVIA University of Applied Sciences in Finland.

His team found that grey owls (pictured above right) have an advantage over brown ones only when there is lots of snow. As winters have become milder, the brown subtype has thrived. It is possible that this is because brown owls are better camouflaged when there is less snow, but it could also be because brown coloration is linked to another characteristic, such as higher energy needs.

There are countless examples of how global warming is affecting life, from plants flowering earlier in spring, to species spreading to areas that were once too cold for them to survive, to birds becoming smaller. The vast majority of these changes are not genetic but due to plasticity: organisms' built-in ability to change their bodies and behaviour in response to whatever the environment throws at them. At least a few species, however, like the owls of Finland, are already changing genetically – evolving – in response to climate change.

In North America, for instance, pitcher plant mosquitoes lay their eggs in pitcher plants and the larvae enter a state of dormancy in the winter months before resuming development in spring. Dormancy is genetically programmed, triggered not by falling temperature but by the shortening days. As the growing season has lengthened, mutant mosquitoes that keep feeding and growing for longer have thrived. Northern populations now go dormant more than a week later than in 1972, when studies began.

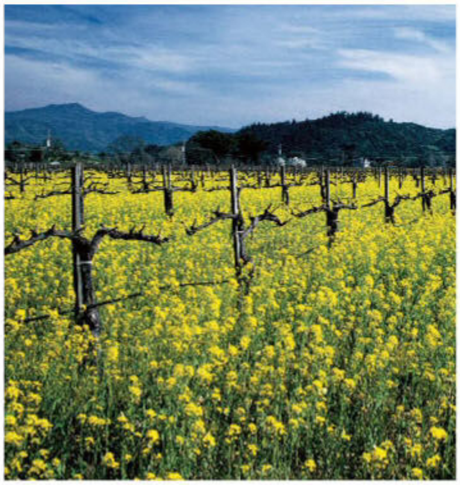
The earlier breeding of red squirrels in North America is also thought to be partly a result of genetic changes. Some families emerge earlier in spring, and they are doing better as the climate shifts.

Plants are changing too. When seed collected from field mustard plants (*Brassica rapa*) in California in 1997 and 2004 were grown in identical conditions, the 2004 strains flowered 9 days earlier on average. The change was a result of drought – the plants have evolved to reproduce before they run out of water.

Rapid evolution is thus already helping some species adapt to a warming world, but it is no "Get out of jail free" card. For instance, so far pied flycatchers in the UK seem unable to shift to laying eggs earlier in spring. And according to one model that specifically takes rapid evolution into account, global warming will kill off 20 per cent of all lizard species by 2080. The problem for lizards is that as the climate warms, they have to spend more time in the shade and less time feeding.

Organisms with long generation times and slow reproductive rates are the least able to

DICK FORSMAN



BRAND X/GETTY

evolve, says Stephen Palumbi at Stanford University. "And they are the ones that are already threatened. It's a double whammy."

Even species whose evolution has kept pace with the slight warming so far will not necessarily keep up as the global temperature soars by another 4 °C or more. Rapid evolution generally depends on the existing variation within a population, rather than on new mutations. "It is limited to the kind of changes that can happen quickly," Palumbi says.

In fact, there is a catch-22 to very rapid evolution – the faster organisms evolve, the less able they are to evolve further. This is because fast change occurs when only a small proportion of each generation manages to reproduce, resulting in a dramatic loss of genetic diversity – the fuel for further evolution. In many cases, the size of populations will also plummet, rendering them vulnerable to extinction. "You could evolve really fast but just not make it," says Michael Kinnison of the University of Maine in Orono.

Plants and animals are being forced to evolve as the planet warms

Poisoning pests

Had any strange itchy bites or rashes recently? You might have fallen victim to bedbugs. The little bloodsuckers are back in a big way, thanks in part to the fact that, like head lice and human fleas, they have evolved resistance to many common pesticides.

Whatever their drawbacks, there is no doubt that pesticides have made a huge difference to our lives. They have helped eliminate diseases like malaria from some areas and made possible the switch to intensive farming. As soon as we started using them, though, resistance began to evolve.

"Insects that succumb readily to kerosene in the Atlantic states defy it absolutely in Colorado [and] washes that easily destroy the San José scale [insect] in California are ridiculously ineffective in the Atlantic states," wrote entomologist John Smith in 1897 – the first known report of insecticide resistance.

The use of synthetic pesticides like DDT took off in the 1940s. Resistant houseflies were discovered in 1946. By 1948, resistance had been reported in 12 insect species. In 1966, James Crow, then at the University of Wisconsin-Madison reported that the count had exceeded 165 species. "No more convincing examples of Darwinian evolution could be found than those provided by the development of resistance in one species after another," he noted at the time.

It's not just bugs. Rats and mice around the world have become resistant to the poison warfarin, and in Europe some have even become resistant to warfarin's replacement, superwarfarin. In Australia, meanwhile, rabbits are becoming resistant to the poison used to control their numbers, called Compound 1080.

Because of its economic importance, pesticide resistance has been studied far more closely than other kinds of ongoing evolution. In many cases we know which mutations are involved, how they make organisms resistant and sometimes even how the mutations spread through populations.

Resistance often arises due to mutations that alter the shape of proteins and thus prevent insecticides binding to their targets. For instance, DDT and pyrethroid compounds kill insects by opening sodium ion channels in nerve cells, but in the malaria-carrying mosquito *Anopheles gambiae*, variants of the channels that cannot be opened this way have evolved on at least four separate occasions.

The other main mechanism of resistance involves enzymes that inactivate pesticides before they can kill. Some resistant strains of *A. gambiae*, for instance, produce large quantities of an enzyme called CYP6Z1 that can inactivate DDT.

Pesticide resistance is becoming such a serious problem that strategies for preventing it evolving in the first place are taken increasingly seriously. One approach is to alternate the type of pesticide applied, to try to avoid applying sustained selective pressure in one direction.

At present, though, the pests seem to be evolving faster than we can develop new pesticides. In one region of Burkina Faso, *A. gambiae* has become resistant to all four classes of insecticides used for malaria control.

Introducing invaders

In 1935, the South American cane toad was introduced to Australia to control pests feeding on sugar cane. The cane fields were not to the toad's liking, but the rest of the countryside was. The toad has spread rapidly at the expense of many native species.

The highly poisonous animals are having a big effect on predators. Some, such as the Australian black snake, are developing resistance to cane toad toxins. Others, such as the red-bellied black snake and green tree snake, are changing in a more surprising way – their mouths are getting smaller. The reason is simple: snakes with big mouths can eat large toads that contain enough toxin to kill them.

The toads themselves are also changing. Some are now colonising regions that were too hot for the founder population, suggesting that they are evolving tolerance to more extreme conditions. What's more, the toads leading the invasion are becoming better colonisers: they have bigger front legs and stronger back legs than toads living in the areas already colonised.

Radio tagging has confirmed that these "super-invader" toads can travel faster, as you might expect. They are probably evolving because the first toads to reach new areas benefit from more food and less competition, and thus have more offspring. The changes are likely to be transient, though – once the toads stop spreading, the "super-invader" traits will gradually be lost.

Ships and planes have turned the natural trickle of species spreading to new islands or continents into a raging torrent, and the new arrivals sometimes have a dramatic effect. In areas of the US that have been invaded by fire ants, for instance, native fence lizards have evolved longer legs. They need them: given the opportunity, a dozen fire ants can kill a lizard in minutes.

Rather than simply study the results of invasions, Michael Kinnison of the University of Maine in Orono and colleagues have been actively experimenting. In one experiment, his team moved juvenile chinook salmon from one river in New Zealand to another. The salmon were introduced to the country around a century ago, and Kinnison wanted to assess the extent to which they had adapted to conditions in individual rivers. He found drastic differences in survival, even though the fish appear identical. "When a population was locally adapted, it performed twice as well," he says.

Kinnison suspects that lots of small changes can add up to make a huge difference to a population's success. "Contemporary evolution may be relatively modest on a trait-by-trait basis, but its overall contribution to the performance of populations may be immense," he says.

Such findings help explain why there is often a lag between the introduction of new species and their rapid spread. A newly arrived species is likely to find itself in an environment that is not quite ideal, and its population may be very small, meaning there is little genetic diversity. In these circumstances, a species will spread only slowly, if at all.

As the population begins to adapt to local conditions, though – perhaps via invisible changes such as mutations in immune genes – it is likely to start to grow and spread. Because more mutations occur in larger populations, it will then evolve faster, enabling it to spread quicker and further. If this turns out to be common, it is bad news. It suggests that many introduced species that seem to be behaving themselves could yet start spreading explosively and cause serious problems.

THEO ALLOFS/CORBIS

Australian snakes can't stomach the poisonous cane toad

Polluting

Between 1947 and 1976, two factories released half a billion kilograms of chemicals called polychlorinated biphenyls (PCBs) into the Hudson river, in the north-east US. The effects on wildlife weren't studied at the time, but today some species seem to be thriving despite levels of PCBs, many of which are toxic, remaining high.

At least one species, the Atlantic tomcod – an ordinary-looking fish about 10 centimetres long – has evolved resistance. "We could blast them with PCBs and dioxins with no effect," says Isaac Wirgin of New York University School of Medicine.

Many of the ill effects of PCBs and dioxins are caused by them binding to a protein called the hydrocarbon receptor. The Hudson tomcod all have a mutation in the receptor that stops PCBs binding to it, Wirgin and colleagues reported in 2011. The mutation is present in other tomcod populations too, Wirgin says, but at low levels.

The most famous example of evolution in action was a response to pollution: as the industrial revolution got under way, cream-coloured peppered moths in northern Britain turned black to stay hidden on trees

Peppered moths turned black during the industrial revolution

ALEX HYDE/BARCROFT MEDIA

stained by soot. As the tomcod shows, though, most evolutionary changes in response to pollution are invisible.

The spoil heaps of many old mines, for instance, are covered in plants that appear normal, but are in fact growing in soil containing high levels of metals such as copper, zinc, lead and arsenic that would be toxic to most specimens of these and other species. The evolution of tolerance has occurred extremely rapidly in some cases, sometimes within just a few years of the soil being contaminated.

With very widespread pollutants, it is much harder to show that organisms are evolving in response, because all populations change at once. The comparison has been done with a common weed called plantain (*Plantago major*), though. Ground-level ozone, produced when sunlight strikes car exhaust fumes, greatly impairs the growth of plants. When researchers grew plantain seeds collected in 1985 and 1991 from a site in northern England where ozone pollution reached very high levels in 1989 and 1990, they found that the plants from the 1985 batch grew nearly a third more slowly when exposed to ozone, whereas the growth of those from 1991 fell by only a tenth.

Since even the remotest parts of the planet are now polluted in one way or another, it is likely that many plants and animal populations have evolved some degree of tolerance, even though few cases have been documented. "Nobody looks for resistance," says Wirgin. "My guess is that if you look you will find a lot of it." His own discovery was entirely accidental: the team had set out to study liver cancers, and they only noticed the tomcod's resistance when blasting the fish with PCBs failed to produce any tumours.

However, there are obviously limits to what evolution can achieve. This is especially true for small populations that reproduce slowly and have few offspring, such as the Yangtze river dolphin. Pollution is thought to have contributed to its extinction.

What's more, pollution resistance in one species can have unexpected consequences for others. The tomcod's tolerance allows it to accumulate extraordinarily high levels of PCBs in its body, for instance, which are a threat to animals higher up the food chain – such as humans with a taste for these reportedly delicious fish.

"The spoil heaps of old mines are covered in plants growing in high levels of toxic metals like arsenic"

Spreading diseases

Perch in Lake Windermere in the UK used to live to a ripe old age. While the average age of fish caught and released by researchers was around 5 years, a few individuals were as old as 20. Then in 1976, an unidentified disease wiped out 99 per cent of adult fish and continued to preferentially kill older fish for years afterwards. Since then, no fish older than 7 have been caught.

According to Jan Ohlberger of the University of Oslo, Norway, the perch (*Perca fluviatilis*) evolved very quickly in response. They now become sexually mature at an earlier age, which increases their chances of breeding before they get killed by the disease.

While the disease is thought to have spread naturally in the lake, Ohlberger points out that many devastating disease outbreaks in plants and animals are a result of human activity. To mention just a few: Dutch elm disease was caused by a fungus introduced from Asia; lions were hard hit by canine distemper spread by village dogs, and corals are far more susceptible to diseases when water temperatures are abnormally high, which is happening often as a result of climate change.

Anything that kills a significant proportion of a population has the potential to bring about very fast evolution. In frogs there is now some evidence of this: last year several research groups reported that some populations appear to be becoming resistant to a fungus that has decimated many amphibian species. It is also clear that human populations have sometimes evolved rapidly in response to diseases such as kuru, which attacks the nervous system.

So it seems plausible that by spreading diseases or creating the conditions in which they thrive, humans are indirectly forcing many organisms to evolve. "I think this is a common phenomenon and has not yet been described because it is simply hard to prove," says Ohlberger. He points out that the long-running capture-and-release programme at Lake Windermere, which began in 1943 and just happened to coincide with the disease outbreak in perch, is pretty unique. In most cases we know too little about what populations were like before disease outbreaks to be able to tell if and how they have evolved in response. ■

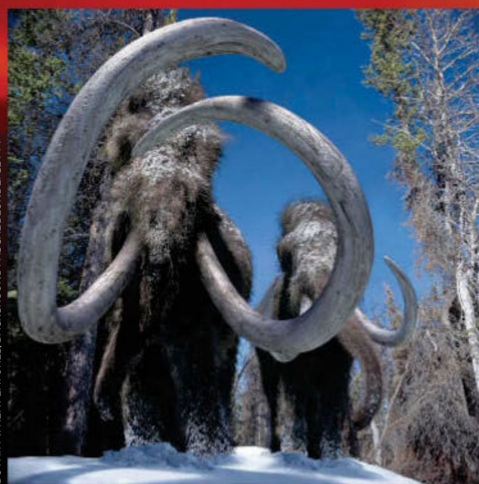
CHAPTER SIX

EXTINCTION

Death on a massive scale

Every now and again, life on Earth faces a crisis. At least five times in the past 540 million years half or more of all species have been wiped out in a short space of time. These mass extinctions are important punctuation marks in the history of life, as once-dominant groups are swept away and replaced with new ones, says **Michael J. Benton**. What triggers this wholesale regime change? How does life recover? And are we in the middle of a mass extinction of our own making?

Woolly rhinos and mammoths died out in an extinction event 11,000 years ago



BOTH: ITV/REX FEATURES; BACKGROUND PASCAL BLONDE/GETTY

WHAT IS A MASS EXTINCTION?

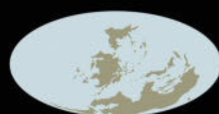
Extinction is a normal part of evolution. Species come and go continually – around 99.9 per cent of all those that have ever existed are now extinct. The cause is usually local. For example, a lake might dry up, an island might sink beneath the waves or an invasive species might outcompete another. This normal loss of species through time is known as the background rate of extinction. It is estimated to be around 1 extinction per million species per year, though it varies widely from group to group.

The vast majority of species meet their end in this way. Most dinosaurs did not die out in the asteroid strike – after 165 million years of evolution, hundreds or thousands of species had already been and gone.

Sometimes many species disappear together in a short time. At the end of the ice ages 11,000 years ago, for example, mammoths, woolly rhinos, cave bears and other large mammals adapted to cold conditions died out across Europe and North America. There have been many such "extinction events" through the history of life.

Occasionally extinction events are global in scale, with many species of all ecological types – plants and animals, marine and terrestrial – dying out in a relatively short time all over the world. This is a mass extinction.

There is no exact definition of a mass extinction. The loss of 40 to 50 per cent of species is about the norm, but this is only the upper end of a spectrum of extinction events. There is no set timescale either: some extinctions happen relatively quickly while others take several million years. It depends on the cause.



Extinction	End-Neoproterozoic	Late Ordovician	Late Devonian
Date	540 million years ago	445-444 mya, in two pulses	375-360 mya, possibly in
Cause	Unknown	Glaciation?	Anoxia?
Genera extinct	Unknown	57 per cent	50 per cent
Major groups lost	Ediacarans	None	Armoured fish

540

Ediacaran	Cambrian	Ordovician	Silurian	Devonian	Carboniferous
NEOPROTEROZOIC ERA	PALAEOZOIC ERA				

600 million years ago | 500 | 400

THE BIG FIVE (OR IS IT SIX, OR SEVEN?)

We now recognise that there have been several mass extinctions over the past 600 million years – the period over which macroscopic life has existed in relative abundance. The first of these was about 540 million years ago, at the end of the Neoproterozoic era (see geological timescale, below), when the enigmatic Ediacaran animals disappeared. Some palaeontologists also identify the late Cambrian as another time of mass extinction.

Three further mass extinctions punctuate the Palaeozoic era. The late Ordovician, between 445 and 444 million years ago, saw substantial losses among the dominant animals of the time: trilobites, brachiopods, corals and graptolites. The late Devonian mass extinction, beginning around 375 million years ago, was another long and drawn out affair. Armoured fish known as placoderms and ostracoderms disappeared, and corals, trilobites and brachiopods suffered some heavy losses. The Palaeozoic ended with the enormous end-Permian mass extinction (see page 116).

Another 50 million years or so passed before the next mass extinction, at the end of the Triassic. Fish, molluscs, brachiopods and other marine groups saw substantial losses, while extinctions on land opened the way for the dinosaurs. They dominated for 165 million years before being wiped out in the most recent extinction, what is today called the Cretaceous-Palaeogene (KPg) event (see page 117).

WHEN THE PENNY DROPPED

Given how important mass extinctions are to understanding the history of life, it may seem surprising that no one was much interested in the idea until the 1970s. Of course, the great Victorian palaeontologists such as Richard Owen and Thomas Huxley were aware that dinosaurs and other ancient creatures were extinct, but they did not see any role for sudden, dramatic events.

Following Charles Darwin, palaeontologists argued that extinction was a normal process: species originated at some point by splitting from existing species, and at some point they died out.

This mindset can be traced back to Charles Lyell, who in the 1830s argued that the foundation of sane geology was uniformitarianism. This holds that "the present is the key to the past": all geological phenomena can be explained by processes we see today, extrapolated over enormous periods of time.

In fact, until quite recently, geologists were conditioned against seeing any evidence of major crises. Woe betide anyone who believed in past impacts and explosions, the marks of an unscientific catastrophist! Until the 1950s geologists even denied that the Earth had been hit by meteorites, arguing, for example, that Meteor Crater in Arizona was a volcanic collapse feature.

This all began to change in the 1960s, a time of ferment and revolution for geologists when ideas of an immobile Earth were rejected in favour of the dynamic reality of plate tectonics.

Arizona's Meteor Crater, the birthplace of impact geology

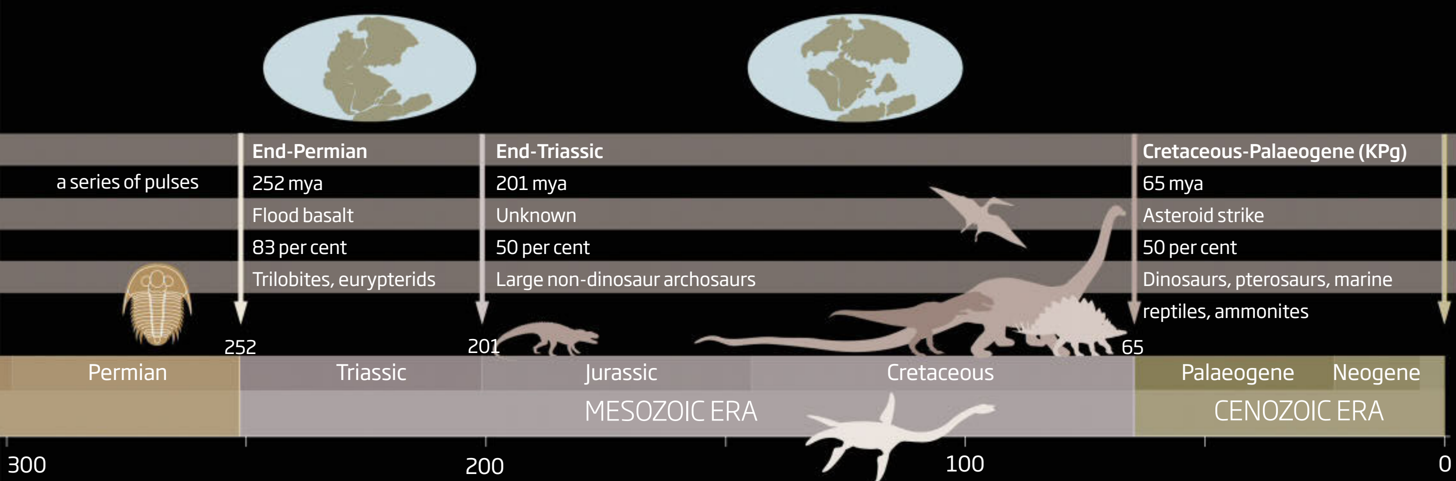
CHARLES AND JOSETTE LENARS/CORBIS

That decade also saw the birth of impact geology. Gene Shoemaker of the California Institute of Technology in Pasadena identified rare minerals, such as coesite and stishovite, in the floor of Meteor Crater, and argued that these were evidence of an impact. At the time such minerals were unknown in nature and had only been created in the lab using enormous temperatures and pressures.

Shoemaker also investigated a large circular depression called Nördlinger Ries in Bavaria, Germany. There he found coesite and stishovite, along with suevite, a type of rock composed of partially melted material. The depression is now considered to be an impact crater some 16 million years old.

Around the same time, palaeontologist Norman Newell of Columbia University in New York began building the case that the fossil record contained evidence of large-scale extinctions. With his work the concept of mass extinctions began to gain currency. Even so, when Luis Alvarez at the University of California, Berkeley, and his colleagues proposed in 1980 that the dinosaurs had been killed off by an asteroid impact the world was still not ready to believe it. Opposition to the idea was substantial, and it took another decade to convince the world that this massive catastrophe really happened.

"Until quite recently, geologists were conditioned against seeing evidence of major crises of any kind"



The terrible two

By their very nature extinction events are a big deal, but two really stand out, one for its sheer scale and the other for its sudden, spectacular and shocking cause

WHEN LIFE NEARLY DIED

The skull of *Dinogorgon*, which died 252 million years ago along with most other animals and plants

One mass extinction truly dwarfs all the others. Whereas earlier and later events each seem to have extinguished about 50 per cent of species, the end-Permian extinction was associated with a loss of 80 to 90 per cent of species in the sea and on land. Several major groups disappeared, including trilobites and giant sea scorpions called eurypterids.

The vast scale of the extinction is shown by the fact that two major structural ecosystems disappeared – reefs and forests. Nothing like that has happened in any of the other mass extinctions.

Reefs first appeared in the Cambrian, and by the Permian had become a major ecosystem hosting substantial biodiversity, as they do today. With the loss of the dominant reef-builders, the rugose and tabulate corals, the Earth was cleared entirely of reefs. It took 15 million years for new groups of coral to evolve and build reefs once more.

Forests likewise virtually disappeared. There is a famous "coal gap" in the early and middle Triassic when no forests anywhere became sufficiently established to produce coal deposits. Key groups of forest insects, soil churners and vertebrates disappeared too.

Such a huge devastation of life might seem to imply a colossal impact. Evidence for this, however, is weak to non-existent. The most-favoured explanation is volcanic eruptions: 252 million years ago, massive volcanoes erupted in Siberia and they continued to belch forth viscous basalt lava and massive clouds of gases for 500,000 years. These were not conventional cone-shaped volcanoes but great rifts in the Earth's crust. The rock from the eruptions now forms a vast formation known as the Siberian Traps.

Sulphur dioxide caused flash freezing for a short time by blocking the sun, but this gas dissipated rapidly. More long-lasting was the greenhouse gas carbon dioxide, which caused global warming and ocean stagnation. Repeat eruptions kept pumping carbon dioxide into the atmosphere, perhaps overwhelming the normal feedback in which plants mop up the excess through photosynthesis.

The warming probably also released frozen masses of methane, an even more potent greenhouse gas, from the deep oceans.

The earliest Triassic rocks contain evidence of repeated cycles of ocean stagnation: their black colour and rich supply of pyrite indicate oxygen-poor conditions. These dark, sulphurous rocks contain very few fossils, in contrast to the abundant and diverse fossils in the limestones just below the extinction level. On land, the volcanic gases mixed with water to produce acid rain. Trees died and were swept away together with the soils they anchored, denuding the landscape. Land animals perished as their food supplies and habitats disappeared.

The slaughter of life in the sea and on land left a devastated Earth. Pulses of flash warming continued for 5 million years, delaying the recovery of life. Some "disaster taxa" such as *Lystrosaurus*, a pig-sized herbivore, gained a foothold here and there, but it took 10 to 15 million years for complex ecosystems to become re-established.

THE DEMISE OF THE DINOSAURS

The extinction of the dinosaurs 65 million years ago, at the Cretaceous-Palaeogene (KPg) boundary, is the most recent of the major mass extinctions and the one most amenable to study. Rocks from before, during and after the event are more abundant, detailed and datable than those for older events. So its cause was just waiting to be resolved.

Up to the 1970s the best evidence suggested that the dinosaurs – along with pterosaurs, mosasaurs, plesiosaurs, pliosaurs, ammonites and many other groups – declined slowly over some 10 million years as a result of cooling climates.

Then came the bombshell. In 1980 Luis Alvarez, who had already won a Nobel prize in physics, his geologist son Walter and other colleagues published an astounding paper in *Science*. The team had set out to use the element iridium as a geological timekeeper, but ended up with remarkably different findings.

Iridium is very rare on Earth's surface, and the minute quantities that are present arrived on meteorites. These hit the Earth at a low but steady rate, so iridium can be used to mark the passage of time: the concentration of iridium in a sedimentary rock indicates how long the rock took to form.

The method worked well when the team applied it to thick sections of sedimentary rock on either side of the KPg boundary at Gubbio in Italy. But at the boundary itself they found a sharp spike in iridium, 10 times the normal amount. If they had stuck to their original hypothesis, they would have concluded that the rocks were laid down by unusually slow sedimentation over a vast time span. But they rejected that in favour of the idea that the spike indicated a sudden influx of iridium from a very large meteorite or asteroid. This, they argued, was what had caused the mass extinction.

The team reasoned that such an impact would have sent up a vast cloud of dust that encircled the globe, blacking out the sun, preventing photosynthesis and so causing massive loss of life. They calculated that a crater some 100 to 150 kilometres in diameter was required, implying an asteroid 10 kilometres across.

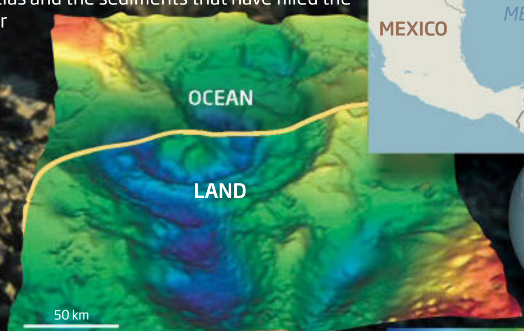
The paper caused an outcry, mainly because it drew such a remarkable conclusion from modest evidence – but such is the stuff of the most daring scientific advances. As the 1980s progressed, geologists found more and more evidence for an impact, including iridium spikes in dozens of locations around the world, the high pressure minerals coesite and stishovite, "shocked" quartz grains, glassy spherules of melted rock and the sudden extinction of many groups of plankton worldwide. Around the Caribbean they also found ancient tsunami debris, and in 1991 the crater itself was identified at Chicxulub on Mexico's Yucatán peninsula (see map, below). As predicted, it was 130 kilometres across.

There are still some serious loose ends to tie up, not least the role played by massive volcanic eruptions on the Deccan plateau of India around the time of the extinction. A handful of geologists dispute whether the impact coincides with the extinction. Even so, the consensus now is that the Alvarez team was right.

Luis (left) and Walter Alvarez in 1985 with a sample of the rock that led to their impact theory

ROGER RESSMEYER/CORBIS

A 3D density map revealing the 66-million-year-old Chicxulub impact structure. The low-density rocks are probably impact breccias and the sediments that have filled the crater



Low density rock High density rock

SOURCE: GEOLOGICAL SURVEY OF CANADA

Patterns of extinction and recovery

Like unhappy families, all mass extinctions are unhappy in their own way. But their aftermaths are surprisingly similar. It takes millions of years, but life eventually bounces back

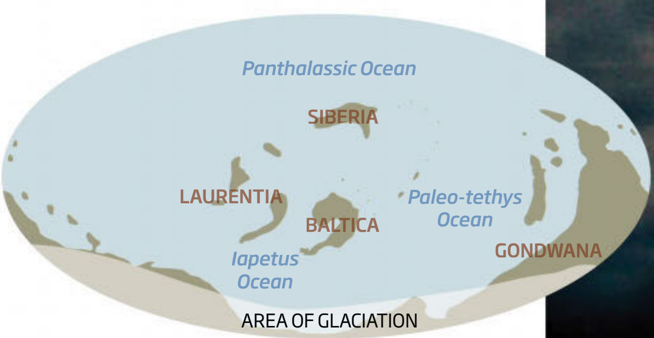
IMPACTS. VOLCANOES. WHAT ELSE?

The causes of two of the largest mass extinctions are now reasonably well understood. But what of the others? In some cases it is difficult to say. The fossil record clearly shows a huge loss of life but not what caused it. Over the years, a number of possibilities have been put forward, but the cause of two of the big five – the end-Neoproterozoic and end-Triassic – remains uncertain.

CONTINENTAL MOVEMENTS. During the Permian and Triassic, all continents were fused into a supercontinent, Pangaea. At one time, the end-Permian mass extinction was linked to this, based on the suggestion that fusion of continents removes intercontinental seas, each with its own unique fauna, and allows land animals and plants to mix. It now seems, however, that such movements are too slow to lead to massive species loss.

ICE AGES. The late Ordovician mass extinction has been explained as a consequence of a massive ice age, particularly the growth of a huge southern ice cap (see map, below). As the ice spread, species migrated towards the equator and warm-adapted species may have disappeared. Sea levels fell dramatically, reducing many inland seas and causing widespread extinction.

ANOXIA. The late Devonian extinction has been linked to a lack of oxygen in the ocean, possibly caused by sudden temperature changes or massive increases in the supply of sediment from the land caused by the rise of terrestrial plants.



IS THERE A COMMON PATTERN?

In the 1980s, as the Alvarez hypothesis gained ground, it seemed reasonable to assume that all mass extinctions were caused by impacts. Though there have been numerous "discoveries" of craters and other impact signatures coinciding with the other mass extinctions, none has stood up to scrutiny. It now seems that the KPg event was unique – the only mass extinction caused by an impact. In fact, we now think that each mass extinction had its own unique cause.

Another idea that was fashionable in the 1980s was that mass extinctions are periodic. Some palaeontologists claimed to have found patterns in the fossil record showing a mass extinction every 26 million years, and they explained this by suggesting that a "death star", dubbed Nemesis, periodically swings into our solar system and perturbs the meteorite cloud. But Nemesis has never been found and evidence for this pattern is now widely doubted.

Common features have emerged, however. For example, it does seem that some species are more vulnerable to extinction than others. Large body size makes animals especially susceptible as it is associated with high food requirements, large feeding range and small population size. Species with specialised diets or limited distribution are also likely to suffer. In contrast, the survivors tend to have large population sizes, live in many habitats in many parts of the world, and have a varied diet.

This is not to say that mass extinctions are highly selective. David Raup at the University of Chicago famously characterised the death of species during mass extinctions as the result of "bad luck rather than bad genes", meaning that the normal rules of natural selection break down. Their success – or lack of it – in normal times has little bearing on their chances of survival when the meteorite hits or the volcano erupts. This holds lessons for current and future extinctions (see page 124). For example, if humans destroy habitats wholesale then all species are vulnerable, whatever their size, diet or habitat.

"In South America, giant birds and crocodilians vied to replace dinosaurs as the top carnivores"

BOTTOM: D.CHAPMAN/WOODFALL WILD IMAGES/NHPA; BELOW: DEAGOSTINI/GETTY

MAIN: ANDREI SPIRACHE/GETTY

LIFE REBOUNDS

Mass extinctions are devastating, and yet life eventually returns to normal. The rate of recovery depends on many factors, but the most important is the scale of the extinction.

After most mass extinctions life recovers within a few million years, though the end-Permian event was different. It was twice as large as most of the others, and so it is no surprise that the recovery time was greatest.

Recovery also depends on which plants and animals survive. If the mass extinction hit all groups more or less equally, as most seem to, then there is a good chance that one or two species from each major group will survive. These act as an ecological framework, occupying most of the broad niches, and so the basic ecosystem structure survives. New species evolve to fill the gaps and the recovered ecosystem may be quite comparable to the one that existed before the disaster.

A more selective event, on the other hand, might leave broad sectors of ecospace vacant. A variety of the survivors then jockey for position, evolving to fill the vacant niches.

After the KPg event it was by no means a foregone conclusion that mammals would take over. Indeed, in North America and Europe, giant flightless birds became the dominant carnivores, some of them famously preying upon ancestral (admittedly terrier-sized) horses. In South America, giant birds and crocodilians vied with each other to become the top carnivores, and mammals only replaced them some 30 million years later.

Mass extinctions, then, have a creative side. Marginal groups sometimes get a chance to expand and become dominant. Most famously, mammals benefited from the demise of the dinosaurs. In fact, mammals first evolved in the late Triassic, at the same time as the dinosaurs, but they remained small and probably nocturnal because dinosaurs occupied all the key niches.

Parts of the post-dinosaur world were briefly ruled by giant birds like *Gastornis* (above), before mammals took over

The end-Permian mass extinction was even more creative, with a yawning post-extinction eco-space providing opportunities for the survivors. In the sea, molluscs (bivalves and gastropods) took over roles previously occupied by brachiopods. Scleractinian corals rebuilt the reefs, and new kinds of light-scaled fish moved into roles previously occupied by more primitive ones. On land, the key beneficiaries of the extinction might have been the dinosaurs, whose earliest ancestors emerged within 5 million years of the crisis.

Noah's nightmare

A flash flood of extinctions is upon us and we cannot save everything. How do we decide which species to target, wonders **Tim Vernimmen**

"ALL animals are equal, but some animals are more equal than others." The famously sanctimonious maxim from George Orwell's *Animal Farm* captures the current state of affairs in nature conservation quite well. Though conservationists are uncomfortable admitting that we might have to let some species go extinct, they also know that it is impractical to try to distribute their efforts evenly.

This makes prioritising inevitable. Every organisation involved in conservation does it, and they often focus on the same species – the cute and the colourful, the ones we feel emotionally drawn to. As a result, most mammal conservation projects target "charismatic" flagship species, leaving three-quarters of endangered mammals unprotected. Birds suffer a similar bias and other life forms rarely appear on the radar at all. But even if we become less emotive in our choices, deciding what to save isn't just about biology – it is political and economic, too. If we want to allocate conservation time and money more effectively, we have some hard choices to make.

Even identifying the species in most trouble isn't straightforward. In the past, they were more likely to be the high-profile animals that still get a lot of attention today. When hunting was one of the main threats of extinction, the species at greatest risk tended to cluster together on the tree of life – carnivores clad in fashionable fur coats or large, tasty herbivores, some with attractive horns or tusks. As global warming takes over as a main driver of extinction, however, this pattern is changing. "Smaller animals may be more vulnerable to climate change than they were to hunting," says Jonathan Davies at McGill University in Montreal, Canada. "And once ecosystems start to collapse, extinctions may appear at random – a classic signal of mass extinctions."

Today, the International Union for Conservation of Nature's (IUCN) Red List provides an inventory of the extinction risk faced by as many species as possible. But with nearly 5000 listed as "critically endangered", just one step from "extinct in the wild", it still leaves the aspiring conservationist spoilt for choice.

One solution might be to focus on areas that harbour the largest number of species – so-called hotspots of biodiversity. However, this can be surprisingly contentious. For a start, it isn't always clear what counts as a species. Where a single species has recently and rapidly diversified into a large group of closely related species, these may not be valued as highly as more distinct species. Likewise, when scientists successfully argue that their favourite species should be split into two or more, some conservationists view this as taxonomic inflation and don't consider the resulting species or subspecies to be as important as long-established ones.

Then there is the problem of judging which hotspots most need protection. It isn't as simple as measuring overall reductions in biodiversity. Although biodiversity is decreasing globally, Maria Dornelas and Anne Magurran at the University of St Andrews, UK, found that on a smaller scale, it is increasing in the sites they looked at almost as often as it is decreasing. But rising biodiversity isn't necessarily a sign that an area is thriving: it may be due to colonisation by alien species that do well in rapidly changing or human-made environments.

Maybe, instead of counting species, we should be looking at the larger branches of the tree of life and trying to preserve regions with high evolutionary diversity. In the early 1990s, Dan Faith of the Australian Museum in ›

Who holds the purse strings?

The total annual global conservation budget in 2005 was around £12.7 billion, according to recent research, equating to some £15 billion in 2014. The lion's share of this – approximately 90 per cent – comes from domestic sources, including governments and self-funding by conservation areas, such as national park entrance fees. There is large variation between countries, however, with governments in low-income countries funding only 13 per cent of their own total conservation spending on average, rising to 97 per cent in the wealthiest countries.

A further 5 per cent of the global spend comes from aid organisations, including the Global Environmental Facility, which funds 22 per cent of this portion, the World Bank (19 per cent) and country-to-country donors, such as the US (7.5 per cent) and Germany (5 per cent). The hardest sector to quantify is private philanthropy and NGOs including Birdlife International, The Nature Conservancy, WWF, and the International Union for Conservation of Nature.

As well as looking at sources of conservation funding, the countries with greatest underfunding were identified, by considering the size of the areas requiring protection and the costs involved in conserving them. Top of the list were Chile, Malaysia, the Solomon Islands and Venezuela.

RICHARD WILKINSON

D. PARER & E. PARER-COOK/MINDEN PICTURES

NATURAL VISIONS/ALAMY

UIG/GETTY

Unusual suspects: the Western long-beaked echidna, Chinese giant salamander and California condor should be high priority for conservation

Sydney devised a way to measure such diversity using phylogenetic trees, a sort of evolutionary family tree where the length of the branches represents the years of evolutionary history separating the species. “It occurred to me that if you were to take such a tree and add up the lengths of the branches connecting all the species in a region, that would give an idea of what I decided to call its ‘phylogenetic diversity’ – the longer the distance, the higher the diversity,” says Faith.

Biological heritage

Together with Félix Forest of the Royal Botanical Gardens, Kew in London, Faith used this approach to assess the flora in the Cape region of South Africa. “We were able to show that areas with high phylogenetic diversity scores may not necessarily contain the most species, but they tend to contain the greatest variety of useful features, such as edible parts, medicinal properties, construction materials and so forth,” says Forest.

What’s more, phylogenetic diversity could boost conservation by creating a source of national pride. “The government in Australia is quite interested in this measure,” says Faith, noting that, with its unusual marsupials and monotremes, the country scores high on phylogenetic diversity. “They would like to add a biological dimension to the notion of what is heritage, so that we might strive to protect not just our cultural heritage, but our evolutionary heritage as well.”

While Faith’s approach allows conservationists to compare the evolutionary history contained in entire ecosystems, it doesn’t tell us about the evolutionary distinctness of individual species, which are still the main focus of many conservation efforts. That’s where the Zoological Society of London (ZSL) comes in. Its researchers have been busy calculating species’ so-called EDGE (Evolutionarily Distinct and Globally Endangered) scores. They first divide the length of each branch of a phylogenetic tree by the number of species at its tip. Then, to assess how evolutionarily distinct (ED) any given species is, they simply add up these values starting at the root of the tree (the ancestral lineage) and ending at the tip where the organism is to be found.

The ED will be highest for those species with a long evolutionary history and few relatives. “This gives you a measure of each species’ individual contribution to the phylogenetic diversity of a region, expressed in millions of years of evolutionary history,” says Samuel Turvey at ZSL. ED is then multiplied with a factor reflecting how globally endangered (GE) it is, based on its Red List status. “The resulting EDGE score allows us to rank animals by phylogenetic uniqueness as well as extinction risk.”

The approach has generated top-100 lists of mammals, amphibians, corals and, most recently, birds, “on the EDGE of existence”, as the EDGE website puts it. “That’s not an exaggeration,” says Turvey. “As soon as we launched in 2007, we found ourselves in the very unfortunate position of having to declare the Yangtze river dolphin – the number one species on our list – to be extinct.” Intriguingly, some of the usual suspects targeted for conservation are well outside EDGE’s mammal top 100, including the tiger (“plenty of other big cat species”) and the African elephant (“not as highly threatened as it was previously thought to be”). “I would never want any resources to be stepped down from existing conservation projects, if these species still need them,” says Turvey. “But we’d like to highlight that there are many other species that also need conservation.”

Whether EDGE chart-toppers represent a good conservation investment is another matter. Some species, including Attenborough’s long-beaked echidna and the New Caledonian owlet-nightjar, haven’t been spotted alive for decades. Might efforts to conserve such species simply be wasting money on evolutionary losers? “That’s a good point, but you have to be really careful there,” says Walter Jetz at Yale University, one of the architects of the bird list. “I wouldn’t dare to call a bird like the shoebill – number 37 – a loser. Yes, it is the only bird in its family, but thanks to its unusual bill, it’s perfectly adapted for cracking certain types of snails, and may therefore play a crucial role in its current ecosystem and, who knows, others in the future.” He believes that if it weren’t for human impact, the shoebill might well be thriving. “And if we lose it, we’ll have to wait at least another 50 million years for such a bird to appear again – if it ever does.”

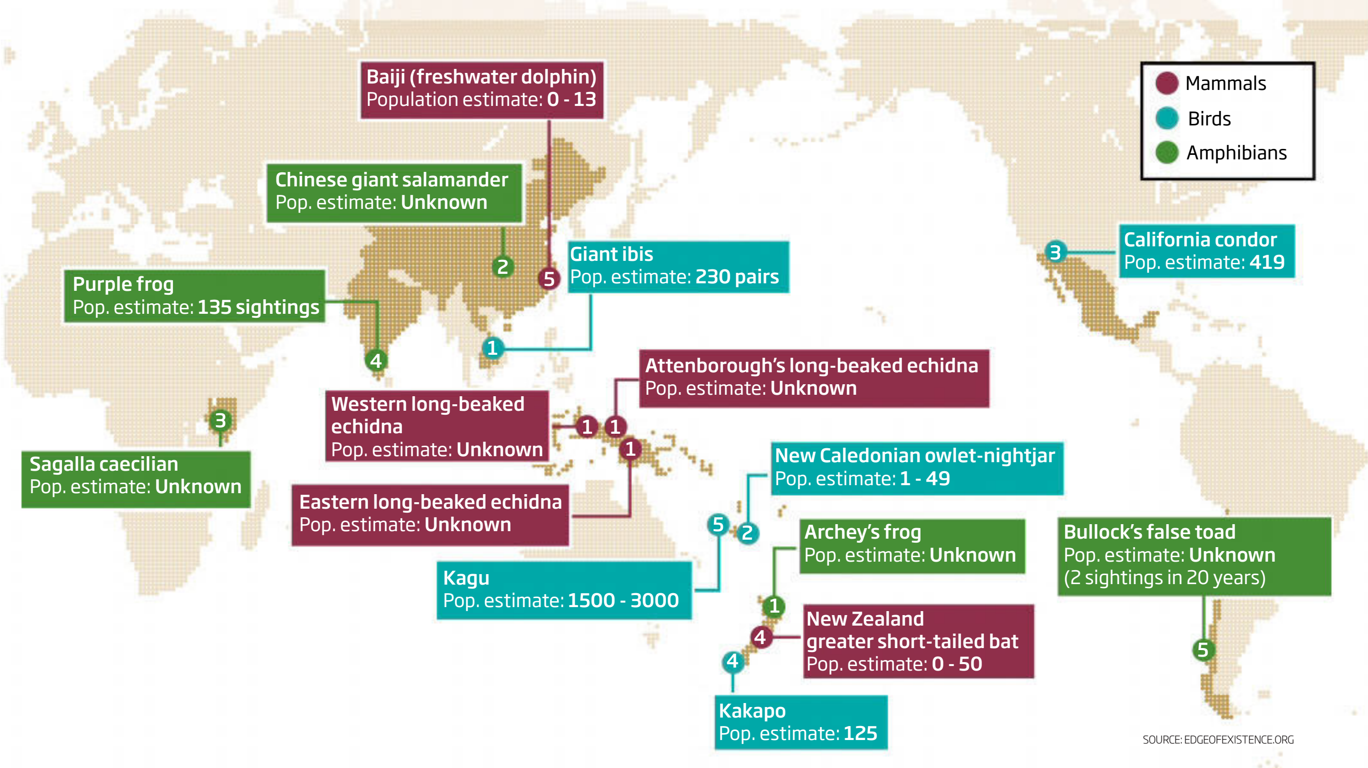
But Faith does worry that by focusing our efforts on the most unusual creatures we risk losing sight of whole branches of biodiversity that might more easily be saved. “I guess it would pay off to consider multiple scenarios and opt for one that doesn’t just maximise the outcome if everything goes according to plan, but also decreases the chance of losing a lot of species if it doesn’t,” he says.

“Obviously, when making decisions about

> “We now have top-100 lists for mammals, birds, and amphibians on the edge of existence”

Not just rare but unusual

With so many species endangered, one approach to conservation is to prioritise those that have few or no close relatives on the tree of life. The species shown here are the top five Evolutionarily Distinct and Globally Endangered (EDGE) mammals, birds and amphibians



how to spend resources, we should always try to get the biggest bang for our buck," says Turvey, "and it is unfortunately true that we don't have enough money or manpower to start protecting all species we'd like to save today." But he cautions against assuming that a species is beyond recovery, because we know so little about the current status or abundance of many on the EDGE lists. Instead of writing species off, he argues, conservationists should be trying to raise more funds from more sources (see "Who holds the purse strings?" page 120). "I think this persistent idea that the amount of conservation resources is fixed is fundamentally flawed," Turvey says.

A more scientific approach to conservation could help rectify that. Jetz has drawn up a map locating the 131 most evolutionarily distinct bird species of the 575 listed as "endangered" or worse by the IUCN to pinpoint places that deserve greater conservation attention. "Interestingly," he says, "the countries that rise to the top are not the ones harbouring the largest number of bird species – that would be Colombia, Peru and Brazil – but places like Indonesia and Madagascar, as well as many smaller islands and mountain ranges, with many unusual and highly threatened species."

Jetz hopes his map will empower these often resource-constrained countries when applying for conservation funding from international organisations such as the World Bank. "It might also generate funds from another source," he adds. "If we could get the birdwatching community to appreciate that seeing yet another white-eye just to add one more species to your list may not be quite the same thing as seeing one of these highly evolutionarily distinct birds, that would be a great way to bring in ecotourism funds to support their protection." Jetz's map is online at Map of Life, a project that brings together information on biodiversity and distributions. The hope is that its attractive design will motivate birdwatchers to share their sightings, providing information to boost conservation.

Beyond the charismatic

With resources such as the EDGE lists and Map of Life freely available, conservationists increasingly have what they need to make more objective decisions and monitor their efforts. So far, the EDGE programme has supported training for some 40 conservation leaders in 25 countries working to protect idiosyncratic species populating its lists, from the pygmy three-toed sloth to the giant salamander. Meanwhile, the IUCN is considering how to take phylogenetic diversity into account when selecting key biodiversity areas on which to target its conservation efforts.

"I think phylogenetic approaches will become ever easier to use, and thus more popular," says Forest. "Technological and conceptual advances make it faster and cheaper to gather large amounts of molecular information from organisms. This allows phylogenetic diversity to be calculated for an expanding range of taxonomic groups and regions." Such expansion should be good news for endangered species that don't qualify as charismatic. Forest and colleagues are currently putting the finishing touches on an EDGE list for gymnosperms, a group of plants that includes conifers, cycads and ginkgos. "I'm curious whether the list will generate a similar amount of excitement as the EDGE lists for animals," he says. "There are some pretty weird and rare gymnosperms out there, and they are fascinating, if you ask me."

Perhaps one day there will be EDGE scores for all life – invertebrates, plants, even microbes. "That would be interesting," says Faith. It would also expose the fact that emotional considerations will always play a part in our choices. "I don't think anybody would seriously consider giving up on a mammal to conserve a larger amount of phylogenetic diversity in beetles or bacteria," he says.

As for the human EDGE score, that is rather humbling. "In terms of evolutionary distinctiveness, we don't even make the top 1000," says Turvey. And when it comes to conservation risk, we are in the "least concern" category, which drops us even further down the list. "Of course we are a serious concern for conservation – but in a rather different way." ■

JULIEN PACAUD

Earth after life

If life – all life – suddenly died, what would be the fate of the planet? Bob Holmes investigates

THE end could come with a bang – a nearby supernova that bathes Earth in deadly gamma rays. Or it might come with a whimper – a supervirus that somehow proves lethal to every living cell on the planet. Neither is remotely likely, but nor are they impossible. Yet thinking about them raises an intriguing question: what would happen to Earth if every living thing were to die tomorrow?

More than you might think. Life is far more than a trivial infestation atop the physical structure of our planet. Living organisms play a major role in a wide range of seemingly lifeless processes, from climate and atmospheric chemistry to the shape of the landscape and even, maybe, plate tectonics.

"The signature of life has gone everywhere – it's really modified the whole planet," says Colin Goldblatt, an earth-systems scientist at the University of Victoria in British Columbia, Canada. "If you take it away, what changes? Well, everything."

Just for fun, then, let's assume that the worst has happened and every living thing on the planet has died: animals, plants, the algae in the oceans, even the bacteria living kilometres down in the Earth's crust. All of it, dead. What happens then?

The first thing to note, actually, is what will not happen. There will be none of the rapid decomposition that befalls dead organisms today, because that decay is caused almost entirely by bacteria and fungi. Decomposition will still happen, but very slowly as organic molecules react with oxygen. Much of the dead material will simply mummify; some will be incinerated in lightning-sparked fires.

Still, the first effects of the wipeout will start to show very quickly, with the climate getting hotter and drier, especially toward the centres of continents. That's because forests and grasslands act as massive water pumps, drawing water out of the soil and releasing it into the air. With no living plants, that pump shuts down and rainfall tails off – all within a week, says climate scientist Ken Caldeira at the Carnegie Institution for Science in Stanford, California.

Water evaporating from plant leaves also helps cool the planet, as though the trees were sweating, so a drier world will quickly warm up. "I'm guessing it might be a couple of degrees," says Caldeira.

In some parts of the world the effect may be a lot stronger. The Amazon basin, for example, depends heavily on moisture released from plants to drive its rainfall. Without the plants, regions such as these could rapidly heat up – by as much as 8 °C, says Axel Kleidon, an earth scientist at the Max Planck Institute for Biogeochemistry in Jena, Germany.

That initial spike is just the start. As the years roll by, the world will continue to get warmer as more and more carbon dioxide creeps into the atmosphere. This happens largely because there are no longer any plankton in the ocean storing carbon in their bodies, dying and sinking down to the depths. As this "biological carbon pump" grinds to a halt, carbon-depleted surface waters quickly come into equilibrium with the carbon-rich depths, and some of this extra carbon finds its way into the atmosphere. The net result is that in as little as 20 years, atmospheric CO_2 roughly triples – enough to raise average global temperatures by about 5 °C, says James Kasting, a geoscientist at Pennsylvania State University.

Plankton will be missed in another way, too, because they release large amounts of a compound called dimethyl sulphide into the atmosphere over the oceans. These molecules act as seeds for water vapour to condense into clouds – especially the low, dense clouds that help radiate heat away from the planet's surface (see "Call in the clouds", page 66). Without plankton, almost immediately, the clouds that form over the oceans will have bigger droplets and therefore be darker, absorbing more heat, says Caldeira. That could contribute another 2 °C of warming within years to decades. On top of the 5 °C from all the extra CO_2, that would be enough to rapidly accelerate the melting of the polar ice caps.

As the world warms, more water will ›

evaporate from the oceans, so more rain will fall. Not everywhere will get wetter, though. Most of the extra rain is likely to fall where it does today – in equatorial regions where converging winds cause air to convect upward, cool and dump its moisture. Wet places are likely to get wetter and desert regions are likely to get drier – not that there will be any living things around to care.

Stripped bare

While all this is happening, Earth will gradually be stripped of soil. No longer held in place by a mat of plant roots, it will be washed away. In hilly environments with plenty of rain, this could take centuries. Flatter landscapes might take considerably longer. In places like the Amazon basin it could take tens of thousands of years, says geomorphologist William Dietrich at the University of California, Berkeley.

All that eroded soil has to go somewhere, and most of it will end up in the ocean, in vastly larger deltas and outwash fans at the mouths of the rivers that take it there.

Rivers, too, will change. The deep-banked, meandering rivers so familiar to us today depend on plant roots to slow the erosion of their banks and keep them from spreading over the landscape. When those roots vanish, rivers will begin cutting through their banks, transforming from a single main channel into a network of braided streams like those seen today in deserts or at the foot of glaciers, says Peter Ward, a geologist at the University of Washington in Seattle. The world has seen this before: during the Permian mass extinction, about 250 million years ago, rivers abruptly changed from meandering to braided.

As the soil disappears, the world will also become sandier. The finer clay sediments so common today are largely a by-product of worms and other organisms that physically break up soil. Without these, the main mechanism for breaking up bedrock will be freeze/thaw cracking and wind erosion, so fragments will be fewer and coarser.

That seemingly small change in particle size, summed over hundreds of thousands of years, will have two big effects. The easiest to see will be changes to the landscape. Larger, coarser particles make for more abrasive sediments in streams and rivers. Over time, these make waterways cut a steeper path to the ocean, and as they steepen so too do the valley slopes. “It’s easy to imagine that you would go to a more jagged landscape,” says Peter Molnar, a geologist at the University of Colorado in Boulder.

Such stream cutting could also get a boost from changes in run-off patterns. Even though less rain and snow are likely to fall on inland regions, the lack of soil to hold the moisture may mean that any that does fall will run off as flash floods. Since most erosion happens during torrential flows, this could mean that in some places rivers will cut down into bedrock more sharply than today even though they carry less water on average, says Taylor Perron, a geomorphologist at the Massachusetts Institute of Technology.

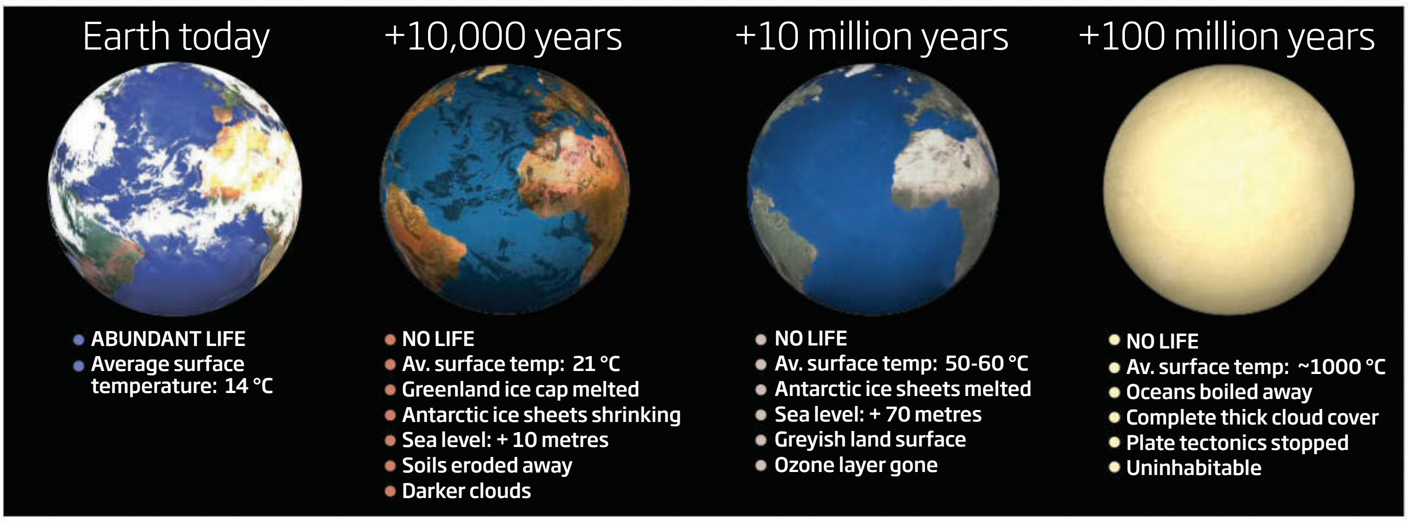
Braided rivers, a tell-tale sign of a landscape with little or no life

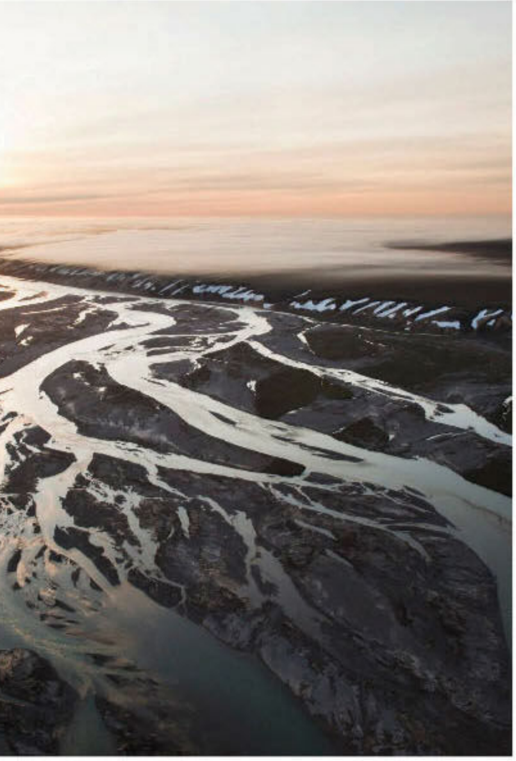
In other places, though, less rain and snow – and fewer glaciers, the swiftest agents of valley-cutting – are likely to lead to less erosion. Whichever way the erosion balance tips, over millions of years it could change the height and shape of mountain ranges by altering the equilibrium between mountain-building and erosion. “It’s not too poetic to say that trees matter to mountains,” says Dietrich.

Still, these changes will be relatively subtle ones. As photos from the surface of Mars show clearly, a world without life wouldn’t appear all that strange to us. “You look at them and you think, well, Arizona, New Mexico,” says

Going, going, gone

Without living things, our lush planet will slowly morph into a hellish inferno resembling our uninhabitable neighbour Venus





SCOTT DICKERSON/CORBIS

Dietrich. "There'd be lots of rock and very little soil. But it wouldn't feel like a foreign planet."

Not unless you check the thermometer, that is, because the increase in the size of eroded and sedimentary particles will make a surprisingly big difference to climate by reducing the rate of chemical weathering of rock – a key feedback in the planet's climate control. Chemical weathering refers to a reaction between silicate rocks and CO_2 to form carbonate compounds. Eventually, these carbonates find their way to the ocean floor, where the carbon is locked away as limestone. Since living things break up bedrock into fine particles, they increase the rock's total surface area and so speed up chemical weathering.

Exactly how much is an open question, but what little evidence there is suggests that life raises weathering rates 10 to 100-fold, says David Schwartzman, a biogeochemist at Howard University in Washington DC. With less weathering, atmospheric CO_2 levels will rise until weathering rates equilibrate again. Over the course of a million years or so, CO_2 levels could increase enough to raise average temperatures from around 14 °C today to 50 °C or even 60 °C, Schwartzman estimates. That is easily enough to do away with all the ice caps.

At the same time CO_2 is building up, oxygen will be disappearing. The early Earth was almost devoid of molecular oxygen, which is far too reactive to survive without steady replenishment. Only after photosynthesis began generating oxygen some 2.6 to 3 billion years ago did this gas begin to accumulate in the atmosphere. After life's demise, it would gradually ebb away. Within about 10 million years, the atmosphere is likely to contain less than 1 per cent of the oxygen it does now, says planetary scientist David Catling at the University of Washington.

At this point there will be too little oxygen to maintain the ozone layer. Without this protective blanket, Earth's surface will be blasted by ultraviolet light. "It would start to be bad in terms of ultraviolet light after 10 to 20 million years," says Catling.

Loss of oxygen will also make the planet a drabber place. Iron-rich rocks will no longer oxidise to their familiar reddish colour. "The surface would get greyer," says Kasting. But there will be highlights. Shiny minerals such as pyrite and uraninite, which form in low-oxygen environments and were common on the early Earth, will resume forming.

An oxygen-free atmosphere rich in CO_2, naked bedrock exposed at the surface of the continents, minerals last formed billions of years ago – that all sounds oddly familiar to Earth scientists. "If you killed off life and waited 100 million years, my guess is that it would look a lot like the planet would if there had never been life," says Caldeira. Others echo his hunch.

Earth's lifeless future may differ from its lifeless past in one important way, though. The sun was about 30 per cent fainter at the beginning of Earth's existence and has been brightening ever since, so the abundant CO_2 in the atmosphere would have been a plus, helping to keep the early Earth from freezing over (see "Under a cold sun", page 20). Under our hotter modern sun, CO_2 is likely to push Earth into a more extreme state.

In fact, Goldblatt thinks that losing life could tip the climate balance entirely. Some models suggest that if temperatures rise enough, the increased humidity in the atmosphere could trigger a runaway greenhouse effect in which higher temperatures lead to more atmospheric water vapour – a potent greenhouse gas – which could raise temperatures still further in a vicious cycle. "Earth today is probably reasonably near that threshold," he says.

It doesn't look like human-made climate change could push us there, Goldblatt stresses. "We're talking about much bigger changes. But we've got millions of years to play with, so I think it's realistic that we could get to a runaway greenhouse." In the extreme, temperatures could rise enough to boil away the oceans, so that the planet could ultimately end up with surface temperatures over 1000 °C. "It may well be that the answer to what Earth would look like without life is Venus," he says.

Others are less pessimistic – if that is the right word when discussing a speculative event hundreds of millions of years in the future. Venus probably became such a hothouse because its plate tectonics stopped early in its evolution, says climate modeller Peter Cox at the University of Exeter, UK. He thinks that Earth, which is still tectonically lively, will continue to bury carbon through subduction of crustal plates, keeping large amounts of CO_2 out of the atmosphere and probably averting a runaway greenhouse.

Trouble could still be lurking around that distant corner, though, because subduction might slow down in the absence of life. Without life, there would be much less of the fine clay sediments that lubricate crustal movement at subduction zones. This could be enough to slow or even halt tectonic activity, says Norm Sleep, a geophysicist at Stanford University in California.

The long-term forecast for our hypothetical sterile Earth is not encouraging, it seems. Without its blanket of life, Earth may not look radically different, but it is likely to become a much more hostile place: hotter, steeper, bathed in radiation and with more severe extremes of rainfall. In the long run, it could end up totally uninhabitable.

Unless, of course, something remarkable happens. No one really knows how life originated the first time round, but it seems clear that it happened within a few hundred million years of the planet cooling enough to be habitable. The same could happen again soon after the extinction event. After all, most of the atmospheric oxygen – a poison to many prebiotic chemical reactions – will be gone, and there could be plenty of organic molecules lying about. Best of all, there will be no pre-existing life to gobble up those tentative early steps – a handicap that may well have prevented a second genesis on Earth.

In fact, a newly sterile Earth – a clean slate – could end up being the best gift a novel future life form could hope for. ■

"If you killed off life and waited 100 million years, my guess is that the planet would look a lot like it would if there had never been life"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